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COLLECTION

CENTRIFUGAL SPECIATION

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INTRODUCTION

MODERN population systematics rests on the assumption that species arise when a parent population is divided into geographical fractions, each isolated from the next by physiographic (or biotic) barriers. During such geographic isolation, the daughter populations can accumulate genetic differences, some or all of which reduce their chances of interbreeding freely and effectively. As soon as these differences accumulate to the point where they constitute a reproductive barrier separating the daughter populations, the latter are then to be considered as newborn species. It must be added that the objective test of a reproductive barrier, and hence of species status, is made only when the daughter populations come into geographic contact. Thus, allopatric populations of obviously close relationship cannot be objectively judged as species or as less than species in the absence of information on their interbreeding reaction. This is the vexing *uncertainty principle* of systematics (Brown and Wilson, 1956).

Geographic separation of populations into potential and then actual species is often assumed to have followed one of two principal patterns.

I. The parent population is split by the intrusion of some feature, usually physiographic, that interferes with breeding between the resulting daughter populations. Barriers usually cited are glacial tongues, zones of aridity, arms of the sea, mountains, areas of high volcanic activity, and the like. We may call this geographical isolation by *division*.

II. The parent population is limited by physically or biotically unsuitable regions that ordinarily prevent its spread. However, under unusual circumstances, a propagule from this population may cross the external barriers and reach a new area favorable to its establishment and subsequent increase. Once the daughter population is safely launched in its new home, its isolation from the parent population may for a time be complete. This process we shall call isolation by *colonization*.

Both of these kinds of geographical separation are frequently invoked to explain the present distributions of species groups, superspecies, and the populations comprising the so-called polytypic species. There can be little doubt that populations are split by such means, or that the result is often a species separation. But it may be a mistake in emphasis to think of these simple processes by themselves as the kinds of species-division most fundamentally important in evolution. It should be questioned that isolation by simple division alone can account for all the overlapping complexities of many continental faunas, or the species swarms in ancient lakes, for instance.

The generally feeble, adaptive, and counter-competitive potential of colonist endemic species on islands (especially when confronted with changes in biotic environment and with new competition) is well-known. It is necessary to question the hypothesis (e.g., Mayr, 1954) that insular faunas may be important potential foci of new major-group evolution, as well as the opinion that species which have evolved on offshore islands as colonists from mainland stocks may ordinarily reinvade "empty niches" on the mainland. The evidence provided by P. J. Darlington (1948, and in press) indicates instead that insular situations are more often in the nature of evolutionary cul-de-sacs, from which there is little chance of important return traffic of species that have been in residence there long enough to have evolved into island endemics. The elaborately radiated geospizine finches of the Galapagos and the drepaniids of the Hawaiian Islands, already showing a rather high incidence of contemporary extinction among their species, can only be considered representative examples illustrating adaptive fragility in insular complexes.

By deprecating the relative importance of simple division and simple colonization as speciation processes, we inevitably raise the question of some other possibilities. One of these alternatives looks so promising that most of the rest of this paper will be spent in discussing it. I refer to the idea that species formation proceeds through a centrifugal progression of variation, and to the supplementary proposition that the process requires density changes and consequent expansions and contractions of geographical range of the evolving population in order to reach completion. Elements contributing to this hypothesis have been both tacitly and openly recognized for many years; some of them are probably as old as the concept of organic evolution itself. I may mention as prominent among contributors to related aspects of "centrifugal theory" Willis (1922), Matthew (1915), Vavilov (1926), Timoféeff-Ressovsky (1940), and P. J. Darlington (1948). There are many others.

So far as I am aware, no one of these authors has dealt with more than a part of what will follow shortly as my hypothesis, and some of them were thinking primarily about the rise and spread of major taxonomic groups, not about the origin of species. Nevertheless, their writings are an indication of a strong and continuing interest in evolution viewed as a central-peripheral succession of taxa. I therefore regard the hypothesis as only the particularized expression of a concept long latent in evolutionary thinking.

THE HYPOTHESIS

The maximum geographical range attained by a species over an indefinite period of time includes areas favorable and also unfavorable for its continuous breeding and increase. Within the maximum range, the populations of the species normally undergo successive expansions into the less favorable peripheral areas, alternating with contractions into more favorable refuges. The expansions and contractions are the sequelae of inevitable density fluctuations affecting all or part of the species at one time. The more important genetic changes tend to be incorporated in the central populations, and are carried outward with these during the phases of expansion. With the phases of contraction, populations of the species disappear from the peripheral areas, except in relatively restricted refugial pockets or islands that are favorable enough to allow survival of some expansion-phase remnants. At this stage, of course, the central populations are geographically isolated from the peripheral remnants, permitting the expected accumulation of genetic differences between them. If, as must happen in only a small proportion of cases, the differences mount to the point of reproductive isolation, the next phase of expansion will establish the geographical contact needed to confirm the new species difference. The new, contiguous, or overlapping species will likely be forced to avoid hybridization (through reinforcement of the reproductive barriers) and competition (through ecological or geographical displacement). The chances are that in most such contacts, the "new central" species will overwhelm the "old peripheral" species by competitive pressure, or, more likely, by means of adaptations of the general "aggressive" type, functioning to remove or incapacitate competitors. But if the two new species can specialize to divide the exploitable environment between them, they may both persist.

The most significant parts of the hypothesis are the emphasis on the center as the principal source of evolutionary change leading to "potent" new species and higher categories, and the role of population density fluctuations in spreading characters and making and breaking the contacts between populations.

ARGUMENT AND EVIDENCE

The maximum geographical range attained by a species over an indefinite period of time includes areas favorable and also unfavorable for its continuous breeding and increase. The truth of this observation is so obvious that we shall not spend time discussing it at length. It should be pointed out, however, that *favorable* areas differ in extent. Other things being equal, the favorable areas of greatest extent should be *most* favorable for the continuing existence of the species, merely because they support the largest total populations year after year.

These populations should have the best chance to originate successful new types through mutation, recombination, chromosomal transformations, gene dispersal, and interdeme selection. The nature and interactions of these processes are the concern of population genetics and are largely outside the scope of this paper. The results of the processes are here generally lumped under non-committal terms such as "character," "genetic change," and so on, and in many cases, this conveys all that is known about them genetically. Whatever their genetic basis, most characters seem to be either directly or indirectly adaptive, so that an area with many exploitable niches available should tend to favor and maintain their variation. The favorability of an area for a given species may indeed be largely a matter of how many niches it includes that are open to the species (Dobzhansky, 1951). At any rate, it seems clear enough that the largest continuous or near-continuous favorable area of a species range is at once the most dependable refugium of a species and the chief fountainhead of its store of variation and general adaptive improvement. Such an area constitutes an *evolutionary center* for the species.

One might expect variation generally to increase from the periphery of the range going inward toward the most favorable areas. However, information on this subject is disappointingly scanty in the literature, probably because the most variable characters are usually of little interest to taxonomists (but see Reinig, 1939; da Cunha, Burla, and Dobzhansky, 1950).

The evolutionary center is, of course, not necessarily coincident with the geographical center of the species range, or with the center of its particular home land-mass. In Asia, North America, and Australia, a large number of species of animals find their optimum situations in the mild, moist eastern parts of those continents, but their ranges often extend far out into the less hospitable central and western reaches of their respective continents. In Africa and South America, the climates most favorable to animal life in general, and thus supporting the largest number of individual evolutionary centers, happen to be near geographical centers of these continents. In such circumstances, geographical patterns of evolutionary change are more free to develop symmetrically in all directions.

In addition to the main evolutionary center, other "permanent breeding areas" may constitute subcenters of varying importance, depending upon their areal extent and the degree of their favorability. These are of lesser importance, since their chances of evolving superior general adaptive types are limited by their smaller resources of variation.

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The journals have accumulated an endless amount of data to show that particular animal species have increased or contracted their ranges within historical times, or even over the span of a few years. Usually these records cover the advance of the most conspicuous or noxious of animals, while the corresponding retreats are, as has already been mentioned, seldom the subjects of documentation. When it comes to determining causal factors behind expansion or contraction, the literature is still less satisfactory. Expansion is most often linked, however uncomfortably, to climatic amelioration, while the arch-destroyer, *Homo sapiens*, is too readily invoked as the cause of range contractions.

In the surprisingly scarce instances where reasonably complete and detailed records are available on expansion-contraction cases among animals, one often finds evidence of density-conditioned processes at work. In general, it seems that animals usually emigrate from "favorable" territory into ordinarily less favorable areas only, or most actively, when population density in the "favorable" or "central" territory threatens to reach a threshold status with respect to some life requisite of the species, such as food. The emigration often appears to be initiated directly by proximate mechanisms that are distinct from, but normally associated in some way with, the ultimate effect having survival value for the population or species (Lack, 1954). In other words, dilution of the central population through emigration may normally be triggered by an incidental density effect, such as physical crowding, or by the interference of an external condition normally accompanying requisite shortage, such as drought. The ultimate effect is to damp increase at a crucial time, checking in advance the last-straw generation that could deplete all of the species requisites and cause a disastrous population crash.

The famous "irruptions" of lemmings, of birds such as the crossbill, and of insects such as plague locusts and the California oak moth provide much studied but by no means unique examples of animals that react to increasingly dangerous density conditions in favorable evolutionary centers by emigrations en masse. Whether most or all animal species "normally" tend to show similar reactions to density increase is of course an unanswered question, and one crucial to the present hypothesis. This question can be answered only by accumulating the proper observations.

In the lemming, mass emigration either precedes or accompanies food shortage, but the proximate cause of emigration in individual lemmings is not yet well understood. Perhaps "derangement" of the type found by Chitty in crowded *Microtus* voles is relevant to the lemming situation. It is interesting to note that emigrant lemmings sometimes establish new colonies beyond the central range (summary in Lack, 1954).

The crossbills are a principally holarctic group of finches, all specialized feeders on the seeds of conifers. Three species are generally recognized (*Loxia curvirostra*, *L. leucoptera*, and *L. pytyopsittacus*), but some of their many "races" may actually be biological species. Most of the populations are given to wandering in search of good cone crops (which are very irregular), and their places as well as seasons of breeding may differ widely from year to year (Griscom, 1937).

From time to time, one or more of these forms engages in a mass irruption that carries large numbers of birds, particularly juveniles, far beyond their usual breeding ranges, and even to remote islands at sea. There is sometimes a smaller return movement, but this usually seems insignificant by comparison with the outward one. The irruptive movements are made in a heightened state of excitability resembling that of the flocking of true migrant birds on the point of exodus, and there are observations to suggest that population densities are more than usually high in the source areas of the irruption. After reviewing the information available for crossbills and several other birds, Lack (1954) concludes that the major irruptive movements are probably initiated proximately by stimuli associated with crowding, and that the ultimate cause is food shortage.

In other words, one can say that in these birds, emigration from the large favorable areas at the distributional center is both density-conditioned and automatically repeated. It seems very significant that crossbills have been established as permanent breeding populations at several remote extralimital points. It will be profitable to return to the discussion of these colonies later, when we take up the subject of geographical variation.

In a discussion of the phase theory of locusts, Key (1950) shows that in grasshoppers and locusts of several genera in different parts of the world, emigratory outbreaks occur, originating in permanent "outbreak areas," regions that are the true continuous-breeding ranges of the respective species. When thoroughly mapped, such an outbreak area may prove to consist of one or two large, central continuous areas about which are grouped smaller ones at varying distances (e.g., Key, 1938).

Density increase in the outbreak area leads to a mutual stimulation among the insects which finally results in the mass emigration of all but a few individuals into surrounding regions where, according to the species, they may either settle or merely feed and move on.

Migratory locusts normally show a transformation in phase, or morphological type, affecting color and structural characters. Frequently, swarming populations will contain largely phase *gregaria;* dilute sedentary populations, phase *solitaria;* and populations in transitional stages, phase *transiens*. But phase condition is mediated by proximate factors of the environment that are in part, at least, different from those chiefly responsible for causing actual emigration. Therefore, phase is not necessarily always well correlated with the condition of the population as regards actual swarming or non-swarming status. Key considers that the function of phase *gregaria* is to intensifiy the effects and coordinate the events leading to swarming.

> . . . there is evidence that transformation into phase *gregaria* has a quantitative effect upon migration which is probably important in connection with outbreaks, at least of some species. Thus it probably makes migration more general among locusts of an outbreak area. It also induces migration before the available food in the outbreak area is consumed, and maintains the migratory urge irrespective of the food supply in the invasion area. The evidence suggests that the phase *solitaria* migrates mainly, perhaps only, when conditions have become unfavorable.

In a most interesting study of the California oak-moth (*Phryganidia californica* Packard), Harville (1955) demonstrates definite, causal correlations between density increase and emigration operating in both the larval and adult stages. The oak-moth females lay their eggs as near the center tops of the oak crowns as possible. The hatching larvae feed for a time in the adjacent foliage, but as they grow, they tend to exhaust the more succulent leaves, which they normally choose by "sample-and-reject" foraging behavior. As they sample more and more leaves, they gradually move outward to the tips of the branchlets, where they exhaust the food supply and finally lower themselves on silken strands. Upon touching a lower branch, they again forage outward and again repeat the descent by silk thread, finally, if the food supply in their path is exhausted, reaching the ground. On the ground, the larvae head off randomly and ascend any object in their way, which for some of them may be the very tree they have just left. After their ascent, the larvae repeat the performance, descending stepwise in their set fashion as the shortage of food drives them, until they either die or get enough nutriment to pupate. In light infestations, however, the larvae may complete their development without leaving the tree upon which they hatched.

The adult females are weak fliers. In seeking a place to oviposit, they are attracted to the upper central portions of oak trees in good foliage, and if such trees are available close by, they will not attempt to travel farther. But if the local oak trees are badly defoliated, the females will avoid them and flutter about rather aimlessly in other directions. Their weak flight renders them particularly likely to be borne along on the wind, and it is chiefly by this means that new colonies are started at distant points.

The oak-moth populations apparently never survive the winter in northern California, and frequently do not in the middle part of the state, though some few favorable localities here may normally support overwintering populations every year. In southern California, one of the two or three larval generations overwinters year after year, and these "central" populations presumably furnish a proportion of the propagules that annually make the colonial starts farther north in the depopulated areas.

So far, only the somewhat "peripheral" populations in the middle part of the state have been closely studied by Harville. These suffer drastic crashes every few years during severe winters, and Harville emphasizes his belief that the eventual replacements building up in the depopulated areas are essentially new populations for these areas.

An interesting case of probable density-reactive emigration is reported by R. L. Chermock (1946) and Nielsen and Nielsen (1950) for the pierid butterfly *Ascia monuste*. This butterfly is widely distributed in the New World tropics, and its permanent breeding range extends to Florida, where it shows seasonal density fluctuations. There is also a drastic longer-term fluctuation occurring irregularly every few years, as judged from observed density of the adults. There seems to be little question that the conspicuous northward and westward emigrations of *A. monuste* are correlated with the higher density peaks. However, the larvae, even during adult population peaks, may have an excess of their normal food-plants within reach. Chermock considered that the proximate point of shortage was the adult food, nectar secured from flowers that seemed to him too scarce to supply all the adults in a given area at once during density peaks.

Chermock's observations were limited and rather casual, but his suggestion that nectar for the adults, and not larval food supply, may be the limiting factor that touches off emigration, should at least serve as a warning to those who consider only "obvious" requisite supplies. *Ascia monuste*, like many another mass emigrant, seems prone to establish colonies outside its permanent breeding range. It also makes conspicuous southward migrations in the southern part of its range in Uruguay (T. Eisner, pers. commun.).

The examples cited above are, I believe, representative of what happens, usually in less spectacular fashion, in a great many if not most animal species. Readers will undoubtedly be able to call up additional instances from their experience in field, laboratory, and literature, and it is here urged that data bearing on emigration be more frequently committed to print.

However, it must be said that opinion is certainly not unanimous on the general importance of the causal relationship between density increase and emigration. Andrewartha and Birch (1954), for instance, ask whether emigration phenomena interpreted as being density-dependent are not often just the normal, proportionate dispersal activities of individuals in any population, rather than the disproportionate tendency to emigration postulated for populations that reach critical densities. Considering the strength of the evidence available in favor of density-conditioned emigration as a common occurrence, the objections of Andrewartha and Birch do not seem to me to offer great difficulty.

Their own favorite example, that of *Thrips imaginis* Bagnall populations in South Australia, is invoked as a case in which observed movements of the animals can be explained without recourse to density-reactive emigration. However, this study seems to me to require confirmation and amplification through additional studies of the total natural history of this species. *T. imaginis* is a very widespread species, the main range of which lies in warmer and more constant climates; the species is known from widespread localities in eastern Australia, New Caledonia, and the Philippines, where it is often abundant (L. J. Stannard, letter, 1956). From this information, it would appear that *T. imaginis* may be existing in South Australia under marginal conditions, and that it may even possibly have been introduced by man. A study of populations in the Philippines or elsewhere in the tropics is clearly called for.

The remarks Andrewartha and Birch make (pp. 123–124) concerning mammal and bird dispersal appear to contain some confusion of proximate and ultimate factors affecting emigration. Their virtual dismissal of mass emigration as an important factor in range extension and extralimital colonization also seems ill-considered considering the evidence available.

The argument over the relative importance of density-reactive influences, and particularly of competition, completely dominates the field of population dynamics today. No two authorities hold exactly identical views, but there is a rather definite division of authors into two opposing schools, one of which (Nicholson, 1954; Lack, 1954) tends to regard competition and density-reaction in general as highly important, while the other (Andrewartha and Birch, 1954; Thompson, 1956) minimizes the significance of these forces My opinions fall closest to those of the first school, provided we can agree on a definition of "competition" that excludes the elements of aggression, dispersal, and adaptation—all of which are seen as *means by which an animal can avoid or reduce competition*, not intensify it (Brown and Wilson, 1956).

Both schools happily recognize that some kind of density fluctuation is a nearly or quite universal quality of populations of animals. The fluctuations can be regular or irregular, and their proximate causes numerous and varied, density-reactive and/or non-reactive. Still, it seems clear that if non-reactive factors assumed to cause all or most of some particular fluctuation are somehow excluded, density-reactive factors in the form of competition will step in to govern populations (Nicholson, 1954). In this sense competition is the ultimate density homeostat, capable of maintaining fluctuation even if other forces fail in this. For our present purposes, we are interested only in satisfying ourselves concerning the inevitability of density fluctuation, however it may be generated.

The more important genetic changes tend to be incorporated in the central populations, and are carried outward with these during the phases of expansion.

I have already made brief mention of the connection between the large, favorable central areas of a species distribution, the prevailingly large breeding populations these will support, and the greater probability that such large populations will give rise to successful new types. This relationship can be supported on wholly theoretical grounds. I believe that it is also reflected in actual data, drawn chiefly from the literature of geographical variation.

We shall take theoretical consideraions first. The genetic changes that mean novelty within a species are introduced at different points in the range, and if they are adaptive, they spread outward from these points. Even if we assume that the range of a species is uniformly favorable, it can be shown that new characters will in one important way have a better chance of arising nearer the center. If we draw a big circle (Fig. 1) to represent the uniformly favorable range of a species, we can place within this some smaller circles to stand for areas over which particular genetic changes (A′, B′, C′ . . . .) have spread. The smaller circles are all drawn at the same size, though of course they would normally vary greatly according to the varying ages and adaptiveness of the characters in a real situation. Since the available evidence indicates that characters usually tend to be distributed without concordance in natural species (Wilson and Brown, 1953), the small circles are spaced evenly. The overlaps (intersects) among the circles, then, represent parts of the range in which the local populations (demes) carry more than one of the changes. The area of heaviest multiple intersection will carry a deme different by a large number of characters from demes of areas where little or no intersection occurs. (See S. Wright, 1956, for related thoughts on "inter-deme selection.")

For the simple reason that there are no centers of character dispersal outside the species range, there exists an outer zone of this range in which intersects will be less frequent than they are closer to the center. (The width and distinctness of the peripheral "zone of intersect rarity" depends on the radius of the character-range circles. The smaller the mean radius of these circles relative to the radius of the whole species range, the more clearcut will be the outer zone.)

From these considerations, it follows that, even in a uniformly favorable species range, the more peripheral demes will tend to be similar among themselves, and individually will differ most from the demes at the very center of the species range. When we apply this concept to real species ranges, the differences in favorability of the included areas should greatly magnify the central-peripheral contrast, provided that other factors do not interfere.

Of course, other factors *do* interfere. When central populations disperse, for instance, they tend to overrun and swamp the peripheral ones, and this process certainly normally opposes central-peripheral differentiation in a most direct and effective way. But even complete swamping of peripheral populations does not mean the total instantaneous disappearance of all peripheral traits. In fact, the persistence of peripherally distributed characters in species ranges now either continuous or discontinuous is good evidence for the central origin of new changes, as is clearly shown by the case of the fire ants, discussed farther below.

We can now examine some cases of variation that appear to follow a central-peripheral pattern. These are drawn from the literature of geographical variation, a literature now very voluminous, and fast increasing. Unfortunately, very many papers that are claimed to deal with geographical variation actually devote most or all of their space to the diagnosis and discussion of so-called "races," subjective entities that serve as much to camouflage as to reveal the variation of individual characters.

I have been forced to draw in the main from the pitifully small minority of papers that do in some measure follow the whole variation in space of individual characters taken separately. There are indications that this documentation could be heavily augmented from examples that are only crudely hinted in the current standard subspecies treatments.

The Barn Owl in Europe

Vous (1950) deals at length with the variation of the barn owl (*Tyto alba*, particularly the male) in the eastern palearctic region. Light-colored populations with sparsely spotted white breast predominate in Britain, western France, Spain, North Africa, peninsular Italy, the southern Balkan Peninsula, and on the Mediterranean islands. In central and northern Europe, darker birds are the rule, with more spots on a darker breast background. In the zone between the predominantly dark and predominantly light populations there exist all degrees of intermediacy between the two extremes, both in the relative frequency of light and dark forms at a given

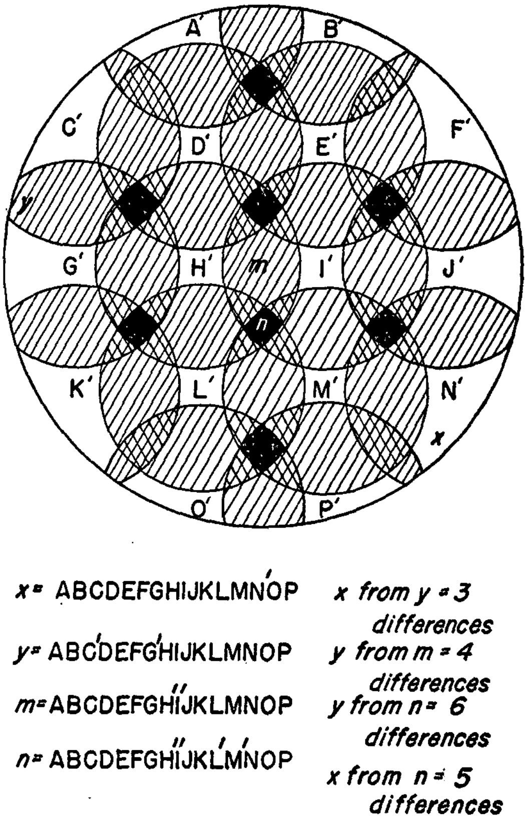

FIG. 1. DIAGRAMMATIC REPRESENTATION OF VARIATION WITHIN AN IDEALIZED SPECIES RANGE

The large circle represents the whole ecologically uniform range of an evenly distributed species population. The smaller circles, marked at their centers by primed capital letters, represent new characters (of the "all or none" type) that have arisen and are spreading at the expense of their respective "normal" versions, assumed to occupy the remainder of the range. Depth of shading indicates the number of new-character circles participating in each overlap. The lower-case italic letters (*m, n, x, y*) are arbitrary sample points chosen to represent demes carrying the character combinations occupying these parts of the range. The letters are used to construct representative character-combination formulae, by means of which the interdeme differences can conveniently be compared. In the formulae, the capitals without primes of course represent the "normal" version of each new character.

locality and in the development of the several independent characters that are involved in the difference. Thus, we have predominantly dark central populations grading out to predominantly light peripheral ones.

Voous notes that the dark condition is apparently spreading outward and that it "dominates" the light condition at the expense of which it spreads. He thinks that the intermediate populations are "hybrid" in origin. The barn owl is a practically world-wide and notoriously variable bird, and it would be interesting to see Voous' analysis extended to the rest of the populations.

Four Cases among the Drongos

Among modern monographs of bird groups, Vaurie's impressive revision of the drongos (Dicruridae) (1949) is rich in data that suggest centrifugal dispersal of characters in the more widespread species.

In one superficially simple case, the African drongo (*Dicrurus adsimilis*) occupies nearly the whole of Africa south of the Sahara. The Congo populations (race *coracinus*) have the mantle and underparts "velvety," and their immatures have indistinct or no light-colored barring beneath. The remainder of the range is taken up by more glossy birds having immatures whitish-barred beneath (race *divaricatus*, northern; race *adsimilis*, southern). Around the velvety Congo population, and between it and the surrounding glossy populations, has been found a broken ring of intermediate samples (race *atactus*) extending even to Principe Island in the Gulf of Guinea (race *modestus*). However, this "intergrade ring" is unusual in its very discontinuous range, and perhaps it is in part merely the reflection of a character displacement system. The velvety and glossy populations meet in some places at the eastern end of the Congo without intergrading. This case needs further study, but whether the velvety and glossy populations are eventually found to belong to the same or to different species, it does seem possible that they conform to the pattern of a central character replacing a peripheral one.

In the Oriental ashy drongo (*Dicrurus leucophaeus*) Vaurie recognizes fifteen geographical races, differentiated mainly on general darkness of plumage color and presence and/or development of facial white marks, but also on general body size and proportions of wings and tail. I have reproduced Vaurie's map (Fig. 2) showing the distribution (by "racial averages") of the two outstanding character variations. It seems to me that the distribution of these characters forms three roughly concentric groupings. At the center, in India and tropical southeastern Asia, there are dark and medium gray populations without white facial markings. Beyond this, an arc of separated populations varies from light gray (northern China) to medium gray (Sumatra and Mentawei). This arc is marked by the decided development, especially at its most remote terminal portions, of whitish facial markings. The third, outermost ring of population is still more widely scattered, occurring on Palawan and nearby Balabac; Java, Bali, and Lombok; and Simalur, off the western coast of northern Sumatra. These populations are medium gray, without white facial markings, and are so similar among themselves that Vaurie (who cannot be called a conservative in the matter of recognizing races) was led to assign them all to a single race, nominate *leucophaeus*.

It is, of course, possible that the characters marking each of the isolates forming the outer rings arose independently (i.e., are polytopic). Another possibility is that the whole pattern marks successive waves of characters spreading outward from the continent. Even the alternation of characters (face unmarked—face with white markings—face unmarked) may be significant, as will be discussed below for the crossbills.

In the greater racket-tailed drongo, *Dicrurus paradiseus*, the birds from India, Burma, and southern China have long, flowing frontal crests. The crest shortens toward Ceylon and toward Sumatra in the south, and finally disappears in the populations on Borneo. On small islands in the south China Sea, in the Andamans, and in Sumatra and Malaya, the crest is absent in varying proportions of the samples available.

Vaurie thinks that the species *D. paradiseus* originated in Borneo, presumably chiefly because the least specialized race occurs there, and that it then moved northward and westward into Asia, producing specialized crested forms at the extremes of its range. In my view, the pattern shows that something like the opposite may have happened. Specializations have arisen on the mainland and are travelling outward *toward* Borneo. In the map (Fig. 3), we see them in mid-passage.

In the spangled drongos (*Dicrurus hottentottus*) there exists an enormously complicated taxonomic picture that may in some respects illustrate cen-

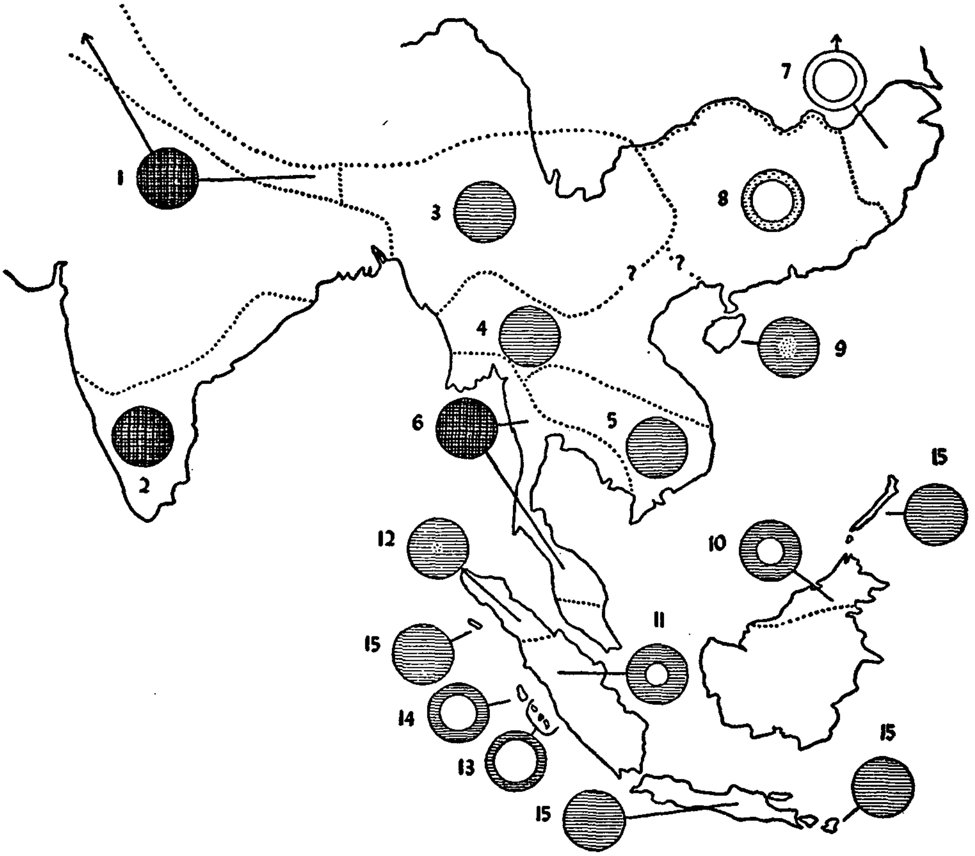

FIG. 2. COLOR VARIATION IN THE ASHY DRONGO, *DICRURUS LEUCOPHAEUS*

The relative degree of general plumage darkness is shown by the full or outer circle, and the relative development of the white facial mark, where present, by the inner circle. Each of the races recognized by Vaurie is represented by a different number. (After Vaurie, 1949.)

trifugal migration of characters. Vaurie's arrangement allows for three groups or "waves" of races, group A being the oldest and most primitive in general character, group B next oldest and derived from A, and C the final, most specialized wave. Group A is the most remote from the Asian mainland, ranging from the southern Philippines through the Moluccas, Melanesia, and northern Australia. Groups B and C replace each other in different parts of the East Indies, C extending onto the mainland of southeastern Asia as far as northwestern India and China. If one considers alternatives to Vaurie's belief that the place where the most generalized races are now found (southern Philippines, Moluccas) is the ancestral home of the species *hottentottus*, the possibility can be entertained that the three waves are centered on southeastern Asia, and that this is the present chief focus of evolution for the species. In view of the findings of Inger (1954) and P. J. Darlington (1948, and in press), it would seem that in other vertebrates the Philippines are more often a zoogeographic terminus than a source of stocks able to expand vigorously to large areas outside these islands.

The distributions of the Asiatic drongos are paralleled in simple fashion by the two very closely related ants *Stictoponera menadensis* (Celebes, Borneo, Philippines) and *S. bicolor* (Southeast Asian mainland). These overlap on Sumatra and Java, and they may not even be specifically distinct (Brown, 1954).

Some Other Birds

Clancey (1955) gives an interesting summary of geographical variation in the orange thrush,

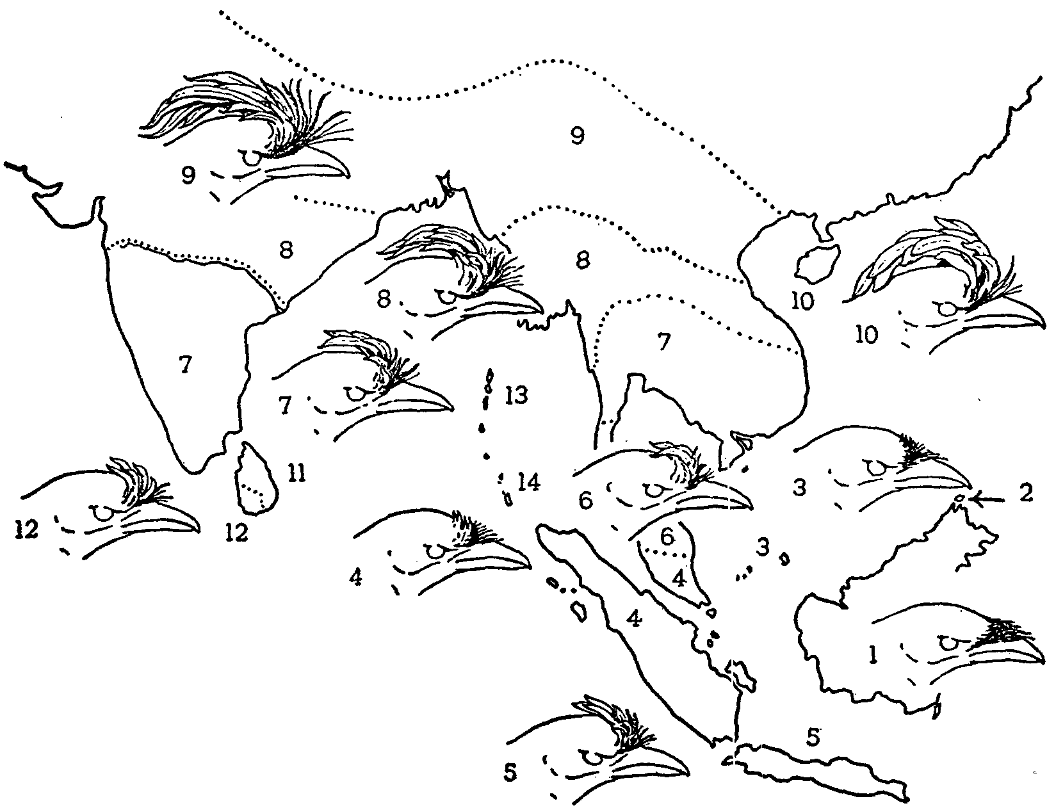

FIG. 3. VARIATION IN THE CREST OF THE GREATER RACKET-TAILED DRONGO, *DICRURUS PARADISEUS*

The numbers refer to the races recognized by Vaurie. The Javanese race *formosus* appears to show a reversal of the clinal trend toward loss of the crest shown by race *platurus* (no. 4) of Sumatra and Malaya, but this is misleading. Most Malayan and apparently at least some southeastern Sumatran samples have the crest about as large as in the Javanese populations; crestlessness is more characteristic of the northwestern Sumatran birds and those from the western Sumatran islands. Treatment of these populations as a single race tends to conceal the very interesting heterogeneity of crest development they show. (After Vaurie, 1949.)

Turdus gurneyi Hartlaub, of eastern and southeastern Africa. This thrush is divided into seven "races," each completely isolated from its neighbors by unfavorable territory, and strung out in line along the highland forests from Mt. Kenya south to Pondoland. He treats these isolates as races, though some or all of them could be distinct species from the data presented. However, it seems reasonably clear that they are closely related membrs of a single stock.

Though we are given only the conventional "race by race" analysis, it is possible in this case to gain a crude idea of some of the independent character variation, especially when Clancey summarizes, and in reference to his map:

> From the discussion on the characters shown by the different populations of *T. gurneyi*, it is concluded that seven racial divisions can be recognised to advantage in our taxonomic arrangement. *T. gurneyi* would appear to be a species of tropical origin which penetrated far into southern Africa during a dispersal optimum, when suitable forests were more extensive and less fragmented in their distribution than at present. This supposition is supported by the fact that adults of the nominate race, which consists of the southern terminal populations, are completely without cinnamon on the rump and upper tail-coverts, though this character is present in the juvenal state, whereas all tropical forms of the species have this salient plumage character in varying degree in the adult plumage. But the new knowledge that the northern and southern terminal populations are larger dimensionally and have larger white wing-spots than those of the five interposed forms, all of which have markedly shorter tails, complicates the preparation of any valid distributional history for the species at the present juncture.

The three characters by which the terminal races differ from the central ones (judging now only from Clancey's data) are the kind of variates that could be allometric in their expression; in other words, variation in size of the white wing spots and in tail length may be tied to general body size, in which case, of course, the characters cannot be considered "independent." If in this case any two, or all three, of the characters are really independent, however, their peripheral distribution would seem even more significant than it does when they are conservatively treated as a single character.

Lack (1953) reviews the geographical variation of the European robin (*Erithacus rubecula*). In central and northern Europe, the robin has a grayish back and a rather pale reddish breast. In some outlying parts of its range, in Britain, the central Canary Islands, Tunisia, and Persia, the birds have a more brownish or olive back, and the breast color becomes a more intense orange-red. The more richly colored peripheral populations are joined to the central continental populations by intermediates in intervening continental areas, although it is clear that the back color and breast color show poor overall concordance in these areas. Except for the central Canaries, the Atlantic islands (Azores, Madeira, western Canaries) all have the pale continental kind of bird at the present time, perhaps a sign that this form is spreading.

A circumpolar passerine, the Lapland longspur or Lapland bunting (*Calcarius lapponicus*) apparently varies clinically (in bill size and lightness of color) both eastward and westward from Greenland, toward Alaska on one side, and toward Europe and Siberia on the other (Williamson and Davis, 1956).

During the autumn in 1953, a strong irruption of these birds reached Scotland and Norway. Judging from the average larger bills and darker color of these birds, as well as from strong meteorological evidence, Williamson and Davis find the emigrants to have originated in the Greenland area. An exceptionally strong influx of this species also reached the southern United States during the winter of 1953–1954, presumably from the arctic areas to the north. This all suggests that population densities in Greenland and the eastern Canadian Arctic were high in 1953, and that a mass emigration in at least two directions derived from this circumstance. There appears to have been no return migration of similar scope in the Scottish area during the spring of 1954. Scotland, Norway, and the United States usually receive migrant Lapland longspurs each winter in much smaller numbers, apparently from Greenland and neighboring American arctic areas.

It is interesting that in this longspur the chief source of at least one major irruption, and also of annual small-scale dispersal movements, should correspond generally so well to the apparent center of observed variation.

The Meadow Frog

The important study by Moore (1944) of variation in the meadow frog (*Rana pipiens*) in eastern North America shows not only that individual characters vary independently and discordantly, but that some of them vary more or less on a central-peripheral plan. The patterns are never exactly the same, of course. The external vocal sacs of the male, for instance, are predominantly well-developed in samples from southern New York and Indiana south to Florida, Louisiana, and Oklahoma. External vocal sacs are usually rare or poorly developed in the northeastern states, Quebec, and in most of the states west of the Mississippi River, including Texas.

Moore's map of the distribution of males with and without oviducts (Fig. 4) shows the pattern typical for a "dominant" and expanding character. In the central part of this sampled area, all male meadow frogs examined lacked oviducts. In the peripheral areas in the west, northwest, north, northeast, and in peninsular Florida, most males have oviducts. However, occasional samples taken in these outer areas do lack the oviducts. Such evidences of incipient swamping of peripheral by central characters are commonly seen in central-peripheral variation.

A Brazilian Legless Lizard

The exhaustive study of the South American lizard *Amphisbaena fuliginosa* by Vanzolini (1951) is a model work that all students of variation would do well to examine. The samples are drawn from widespread localities in the northern half of South America and Panama. Seven diverse characters are studied independently, each for the entire range, and an attempt is made to synthesize the conclusions. The final result is the delineation of five "races," but in my opinion these add nothing to the very thorough basic analysis, and they would probably be misleading if taken without it.

The variation of the seven characters is discordant and uneven for the most part, but two of

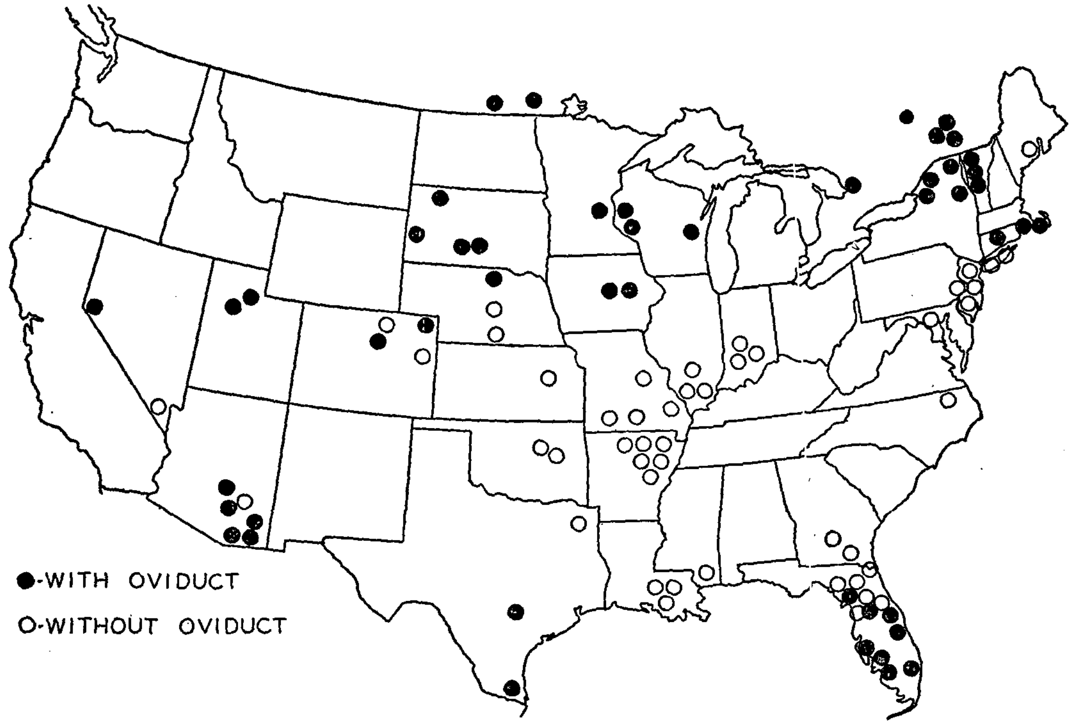

FIG. 4. DISTRIBUTION OF MALES OF THE MEADOW FROG, *RANA PIPIENS*, WITH AND WITHOUT OVIDUCT

Samples are from the United States and adjacent parts of Canada only, though the meadow frog has a much wider range in North and Central America. Each dot or circle represents 1 to 4 male frogs dissected; those in Vermont, New Jersey, and Long Island represent much larger samples. (After Moore, 1944.)

them do seem to show a rough sort of agreement in their distribution. These, number of body annuli and relative length of tail, follow strongly central-peripheral patterns. The body annuli (Fig. 5) show high counts in the area of Manaos, and drop off from this in all directions, most rapidly toward the northwest (Colombia and Panama). An arc of similar counts stretches from Peru around the northern Brazilian border to the Guianas and Trinidad.

The tail-length variation is strikingly similar in most details to that of the annuli, but here the central Amazonian values are low, and those surrounding are higher. Considering all characters together, Vanzolini finds that the Peru-Ecuador ("*bassleri*") populations are more like those of the Orinoco-Guianas area ("*fuliginosa*") than these are like the intervening Amazonian populations called "*amazonica*."

> . . . although *A. f. amazonica* has a range situated between those of *bassleri* and *fuliginosa*, its characteristics are not intermediate between those of the named forms. On the contrary, *bassleri* and *fuliginosa* are very closely related forms, differing chiefly in color.
>
> This situation could have arisen in two ways: (a) *amazonica* giving rise to two convergent forms in different parts of the range; (b) *amazonica* being the result of the evolution of a population occupying the central part of a territory, on the fringes of which the primitive stock suffered further but less extreme differentiation.
>
> If we consider now [the Colombia-Panama and eastern Brazilian populations] we see that they approach more closely the forms with low counts of body annuli (*bassleri* and *fuliginosa*) than *amazonica*. In this manner I believe the second hypothesis listed above is the more probable. . . .

The New World Fire Ants

In the cosmopolitan ant genus *Solenopsis* the most notorious pest species are the members of the neotropical *geminata* group (subgenus *Solenopsis*). *S. geminata*, a species whose original range lay in the circum-Caribbean countries, has spread widely over the tropics of both hemispheres. *S. xyloni*, a widespread southern nearctic species, appears largely to have been replaced by *geminata* along

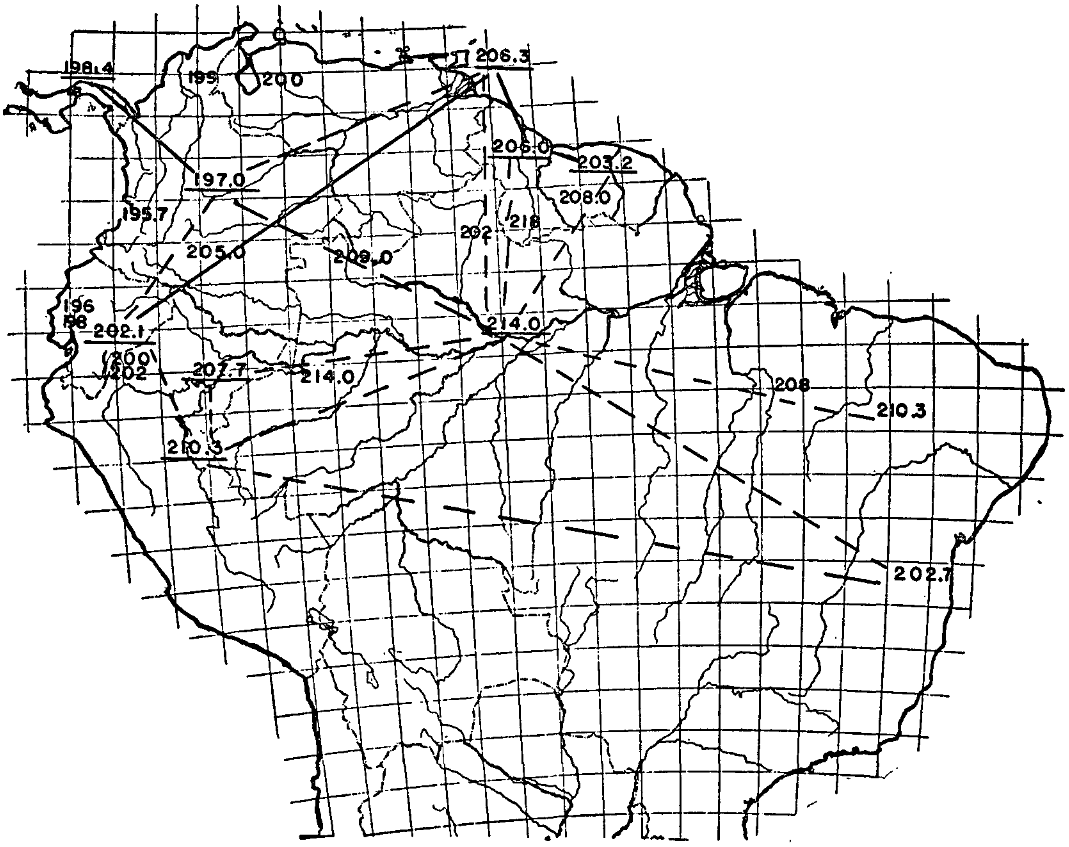

FIG. 5. GEOGRAPHICAL VARIATION IN THE NUMBER OF BODY ANNULI OF THE LEGLESS LIZARD *AMPHISBAENA FULIGINOSA*

Decimal numbers represent the number of annuli averaged for a sample from the place indicated. Numbers underlined are the nine major samples; others are smaller samples of 3 or 4 individuals each; integers represent single specimens. Numbers connected by solid lines do not differ by a statistically significant amount; broken lines indicate a statistically significant difference between the numbers they connect. (After Vanzolini, 1951.)

the coastal strip of the Gulf of Mexico wherever the latter is common.

At about the time of World War I, a third species of the same group became established at the Gulf port of Mobile, Alabama. This ant was identified with the dark Argentinian population of *S. saevissima*, the predominant species of the group from the Guianas south onto the Pampas.

> For about ten years [the Mobile population] remained both genetically homogeneous, corresponding to the dark southern race *richteri* Forel of the South American parental population, and relatively unsuccessful in its new surroundings. In the period following 1930 a smaller reddish form rose to abundance, interbred extensively with the original dark form, and apparently precipitated the species' explosive increase to pest proportions. By 1949 the reddish form had largely replaced the dark form, which had become limited principally to the southern strip of the main population and part of its eastern and western periphery and to two outlying, isolated populations in Mississippi. (Summary by Wilson, 1953).

Wilson found that over its native South American range, the yellow "typical" *saevissima* population of northern and central Brazil, gives way to the Argentinian black form through a broad clinal zone including Bolivia, the Chaco, and southeastern Brazil. The post-1930 reddish form of the Mobile area matched samples from the South American intermediate populations, and may well have arisen as a second introduction from southern Brazil or northern Argentina.

The map (Fig. 6) shows Wilson's plot of the growth of the main North American area of infestation through 1949; several smaller centers had

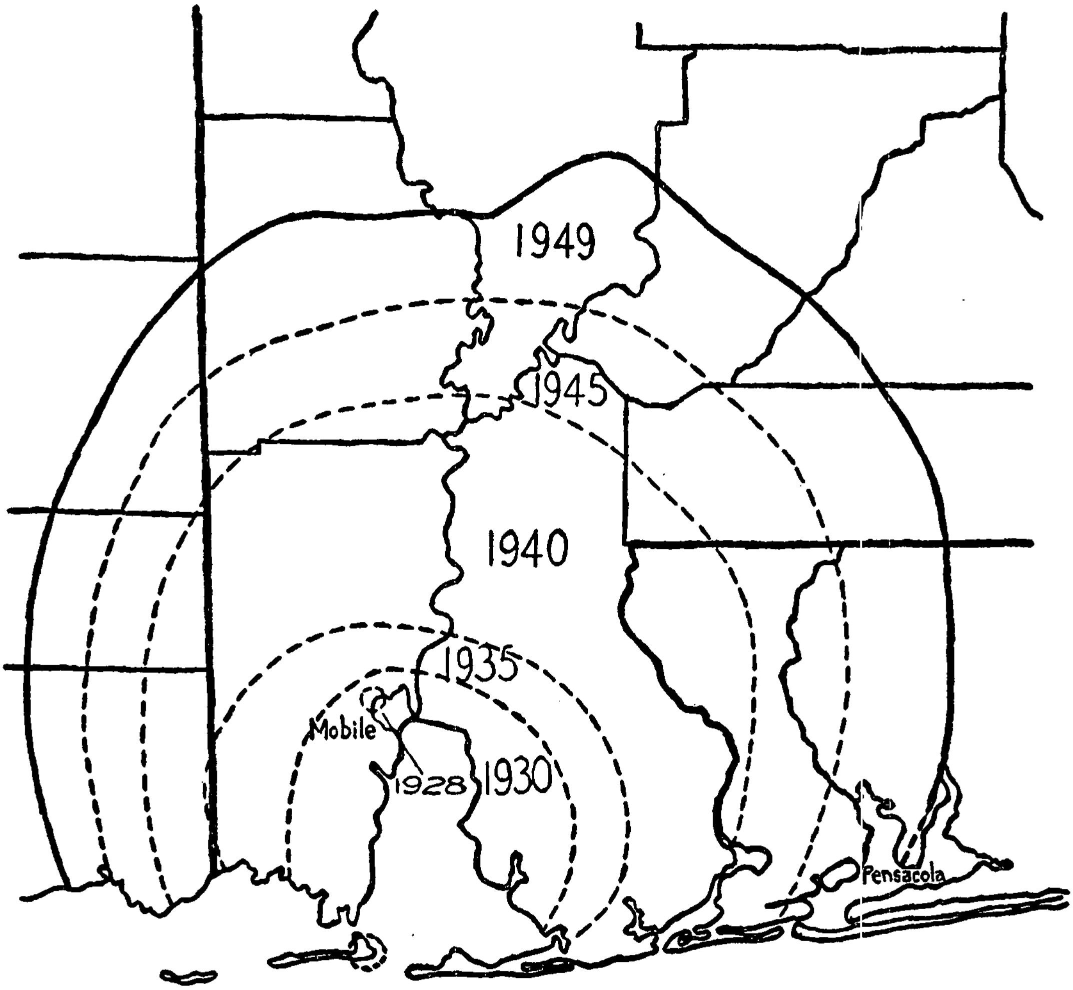

FIG. 6. ESTIMATED RATE AND DIRECTION OF SPREAD OF THE MAIN AREA OF SPREAD OF THE IMPORTED FIRE ANT, *SOLENOPSIS SAEVISSIMA*, IN THE CENTRAL GULF COAST REGION OF THE UNITED STATES, AS OF 1949

There were a number of smaller infested loci outside the main area in 1949, and many of these have since been engulfed by the spreading main area, according to recent surveys. (After Wilson, 1951.)

by that time become established a little farther north and west outside the main area, apparently most of them started accidently after transport by human commerce. Since 1949, the U. S. Department of Agriculture (Culpepper, 1953) has reported a considerable spread of the infested area, but the present proportions of light and dark phases remain unrecorded, except for a limited coastal area south of Mobile. Here in 1956 Wilson (pers. commun.) found during a brief survey that the frequency of dark-phase nests appeared to be lower than in 1949. Particularly did it seem to him that young dark-phase nests were scarce or absent in this region, so it may be that in their incipient stages, the dark-phase colonies are vulnerable to competition or aggression by the red phase.

The dark-phase colonies apparently are now limited to certain separated peripheral areas of the range and a few minor enclaves within the main area of infestation, and even where they occur, they are often in the minority (Fig. 7). All degrees of intergration link dark and red phases. As the red forms press outward, the dark forms apparently suffer both genetic swamping and competition-aggression, and consequently tend to extinction in most habitats. In spite of these forces at work against it, the dark form persists, genetically embedded, so to speak, in the dense and

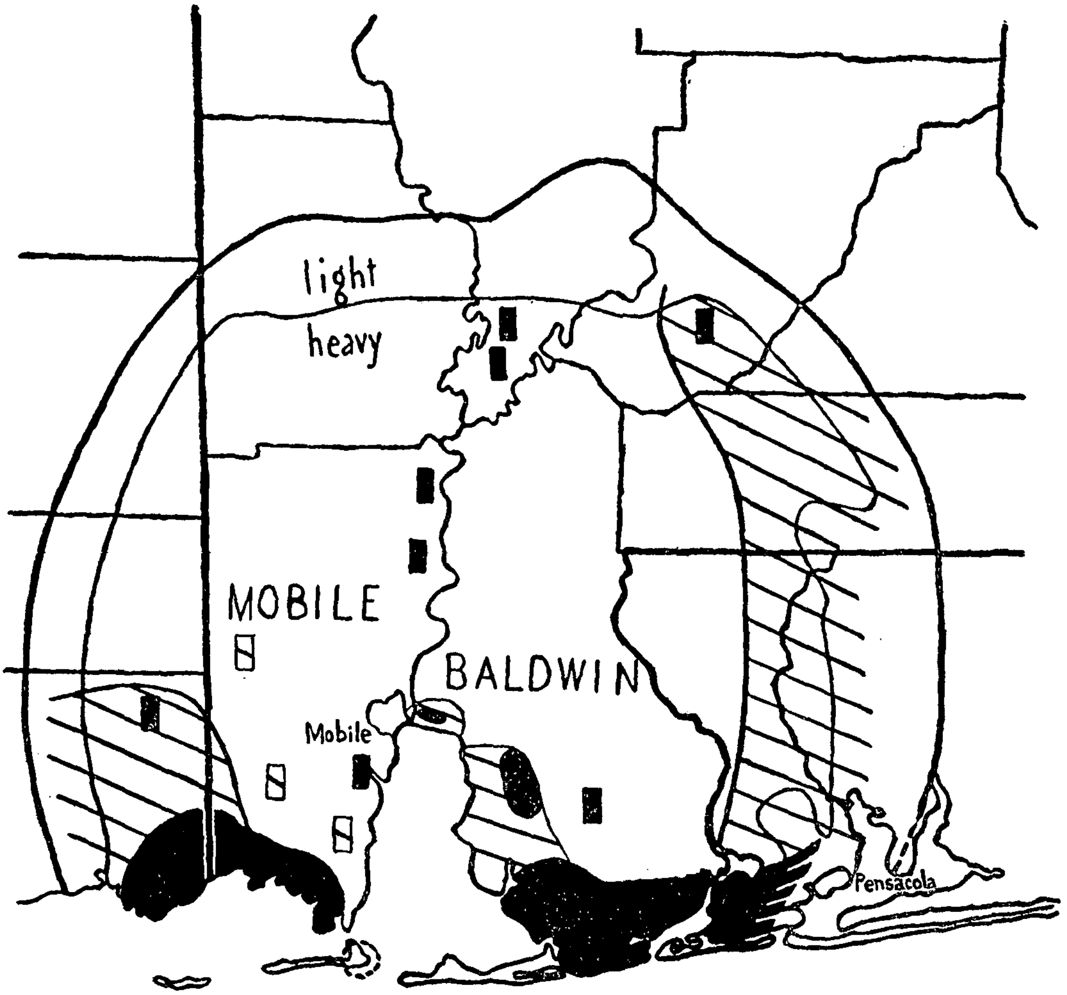

FIG. 7. DISTRIBUTION OF THE COLOR PHASES OF THE IMPORTED FIRE ANT IN THE MAIN AREA OF INFESTATION, AS OF 1949

Solid black represents areas with incidence of dark and intermediate phases of greater than 20 per cent; hatching represents areas with incidence of these phases of 5–20 per cent. Small black rectangles represent minor isolated dark-phase populations. In the centers of infestation outside the area shown in 1949, some populations were dark, others light; the present status of these is unknown. (After Wilson, 1951.)

expanding matrix of red populations. This case is very instructive in showing how, regardless of its origin in this particular case, a genetic change actually spreads from a central point of introduction and tends in this way to cause a central-peripheral differential.

It is also interesting to note that *S. saevissima* occupies a large, favorable central range with respect to *S. geminata* and *S. xyloni* in the New World. In the area of infestation in North America, *S. saevissima* has almost completely replaced its two congeners in areas where one or both were formerly abundant.

A perhaps even more remarkable case of centrifugal waves of change passing through a species range is that claimed for the land snail *Partula vexillum* Pease on Moorea in the Society Islands. Crampton (1932) believed that the evidence shows this snail to have alternated between dextral and sinistral types at least once, and perhaps twice, during a half century. He showed that the changes probably have taken place in centrifugal waves from a common center in the southern part of the island. This snail will bear watching in years to come.

Color Variation in the Common Hornet

Professor J. C. Bequaert has shown me the interesting color variation in the common Eurasian hornet (*Vespa crabro* Linnaeus). On the European Continent and eastward through Asia Minor and Siberia, the hornets are dark in color ("vars. *crabro, germana,*" etc.), with brownish or dull russet occiput and with the brown part of the second gastric tergum usually unrelievedly dark. In England, and then again in eastern Asia, in a broad zone extending from Manchuria and Korea south into Thailand, the color of the occiput is a clear yellowish, and many of the specimens show a broad yellowish-brown fascia within the brown part of the second gastric tergum.

The occipital color is not perfectly concordant in geographical distribution with that of the gaster, but yellowness on head and gaster tends to be more common in the British and the southern and eastern peripheral parts of the species range (Bequaert, 1931).

It is interesting to note that this hornet has been introduced into eastern North America, where it is now rapidly spreading. The immigrant populations are dark in color, corresponding to the central European population ("var. *germana*"). The Japanese hornets are darker in general than those from the Chinese and Korean mainland; Japan apparently is influenced chiefly from eastern Siberia, lying directly to the north.

Butterflies and Moths

In the New World tropical ithomiine butterflies of the *Melinaea lilis* complex, Forbes (1927) finds that "advanced" variants are more centrally located, while peripheral forms at opposite distributional extremes may closely resemble each other. He thinks that this situation "may be due to a more advanced form taking possession of the center of distribution, and driving the earlier types to the margins."

As dealt with by Forbes (1927, and pers. commun.) the *Melinaea lilis* complex consists of several named forms, distributed roughly as follows, from north to south:

imitator Bates	S. Mexico, northern Central America
scylax Salvin	Costa Rica
parallelis Butler	Panama
messatis Hewitson	Colombia
lilis Doubleday and Hewitson	Venezuela
dodona Hopffer	Peru, etc.

Of these, *scylax* may possibly be a species distinct from *lilis*, but this is uncertain. The geographical forms *parallelis* and *messatis* are hardly separable from each other, and feature a large black apical section of the forewing with usually three rows of small white spots. The dark longitudinal stripes of both wings are largely restricted to the apical portions. The *parallelis-messatis* condition grades into *lilis* in Colombia-Venezuela; *lilis* has a smaller black apical section of the forewing enclosing two rows of yellow streaks or elongate spots, and in addition, each wing bears two longitudinal dark stripes reaching to near the wing base on the orange field. The northern population (*imitator*) is almost precisely identical to Venezuelan *lilis*.

[In the clines *messatis-lilis-dodona*, these diagnostic characters of the "races" change one at a time, and not in geographical concordance. Fox (1955) intimates that his studies in the Ithomiinae have failed to reveal discordant geographic variation in this group, although he cites no examples. It is therefore of interest that Professor Forbes, long a student of the ithomiines, has been able to furnish evidence of discordance in *M. lilis* purely as a chance incident to the present study.]

Other possible cases among the Lepidoptera occur in *Papilio thoas*, in the migratory *Vanessa*, and in the moth *Eacles imperialis*.

The Marsh Fritillary (*Euphydryas aurinia*) of the British Isles has a peripheral form (*praeclara*) in Ireland, and transitional types are found in the western isles of Scotland. It is this butterfly upon which Ford and Ford (summary in E. B. Ford, 1945) made their now widely appreciated observations on population fluctuation and variation. A record of an isolated English colony of *E. aurinia* was kept back to 1881, and high density peaks occurred during 1894–1897 and 1925 to beyond 1935. The later peak was reached by a rapid increase in numbers after a long period of scarcity. During this increase period, the variation widened explosively to produce all sorts of extreme variants, including some deformed individuals. After the rapid increase stopped, extreme variants disappeared and the colony settled down to a more homogeneous type. This type, however, differed somewhat from the one prevailing during the earlier population peak.

Observations of this sort are regrettably rare, considering their interest and importance, but now population genetics is inevitably entering a period of detailed investigation of density-reactive variation (see discussion of *Drosophila pseudoobscura* group below). We especially need information on the variation of strongly emigratory animals as correlated through time with density peaks and troughs.

Adaptive Inversions in Drosophila

Drosophila of the *willistoni* group are among the wild fruit-fly predominants in tropical America. America. *D. willistoni* itself is a very common and widespread species, ranging from Florida and central Mexico southward to Argentina. Some 40 identifiable chromosomal inversions have been found in *D. willistoni*, and their frequency at any given locality has been linked to the probable number of ecological niches exploited at that place by this species. Thus, the number of inversions is highest in central Brazil, in regions where luxuriant rainforest and savannah interdigitate, and where *D. willistoni* far predominates in numbers over its three sibling species (*D. paulistorum*, *D. tropicalis*, *D. equinoxialis*). But the numbers of inversions present in *D. willistoni* fall off toward the northern (Central America) and southern (southeastern Brazil) extremities of the range, and drop drastically in local regions of eastern Brazil that are ecologically unfavorable for the species. The *D. willistoni* inversion counts are also lower in certain localities in the Amazon Basin that are ecologically favorable, but in which one or more of the three sibling species have reached a high frequency; this may be "character displacement" at the level of chromosome morphology (da Cunha, Burla, Dobzhansky, 1950).

These same authors indicate that the left limb of the X chromosome in *D. willistoni* may show peripheral similarities in its inversions.

> XL is the most "difficult" chromosome, owing chiefly to the prevalence of the geographically different gene arrangements. Crosses of the standard strain to strains from south Brazil usually give the quintuple inversion . . . (B, D, F, G, H), while the triple inversion (B, C, D) is observed in crosses of the standard to Central American (Costa Rica, Guatemala, Mexico) strains. The quintuple and the triple inversions have two elements (B and D) in common, which means that with respect to these two inversions the Central American and the South Brazilian strains are actually more similar than either of them is to the standard strain which is of geographically intermediate origin.

In breadth of range, in average overall abundance and dominance, and in numbers of inversions present, the four species of the *willistoni* subgroup have the relation *willistoni* > *paulistorum* > *tropicalis* > *equinoxialis*. For the most part, these species have appeared to possess concentric range boundaries centered on equatorial Brazil, with *D. equinoxialis* the most limited in extent and *D. willistoni* the broadest (Burla *et al.*, 1949; Dobzhansky, Burla, and da Cunha, 1950). This would appear to be the opposite kind of situation to the central-peripheral ones we have been discussing, and therefore not easy to explain unless we allow that such "niche-rich" areas as tropical Brazil may provide the best refugia of all due to mosaic discontinuities of their biota. But now Townsend (1954) has found populations in the Greater Antilles that he assigns to *D. tropicalis* (as a "subspecies *cubana*") and to *D. equinoxialis*, as well as to *D. willistoni*. It is clear that much remains to be learned concerning the distribution and taxonomy of the *willistoni* sibling species before we can understand exactly what the situation is here with respect to "relict" forms. If investigations continue over the years, it may be possible to chart some interesting evolutionary changes in this complex. More attention should be paid to *D. nebulosa*, a *willistoni* group member that tends to have a peripheral distribution and is more xerophilic than *D. willistoni*, so that the ecological and geographical distributions of the two are roughly complementary.

North American Camel-crickets

Hubbell (1936, 1954, 1956) calls attention to two most interesting "centripetal clines" in characters of two North American species of the orthopteran genus *Ceuthophilus*. The case of *C. uhleri* Scudder is described in detail:

> This wingless camel-cricket is a species of the eastern deciduous forest region, ranging from Iowa and Kansas east to southern New York and coastal Virginia, and south in a narrowing wedge to the Gulf Coast in Alabama and Florida. It shows a centripetal pattern of clinal variation in two characters of the genitalia [Fig. 8], one of the sternum, and one affecting the proportions of the legs and their spinous armature. Populations in-

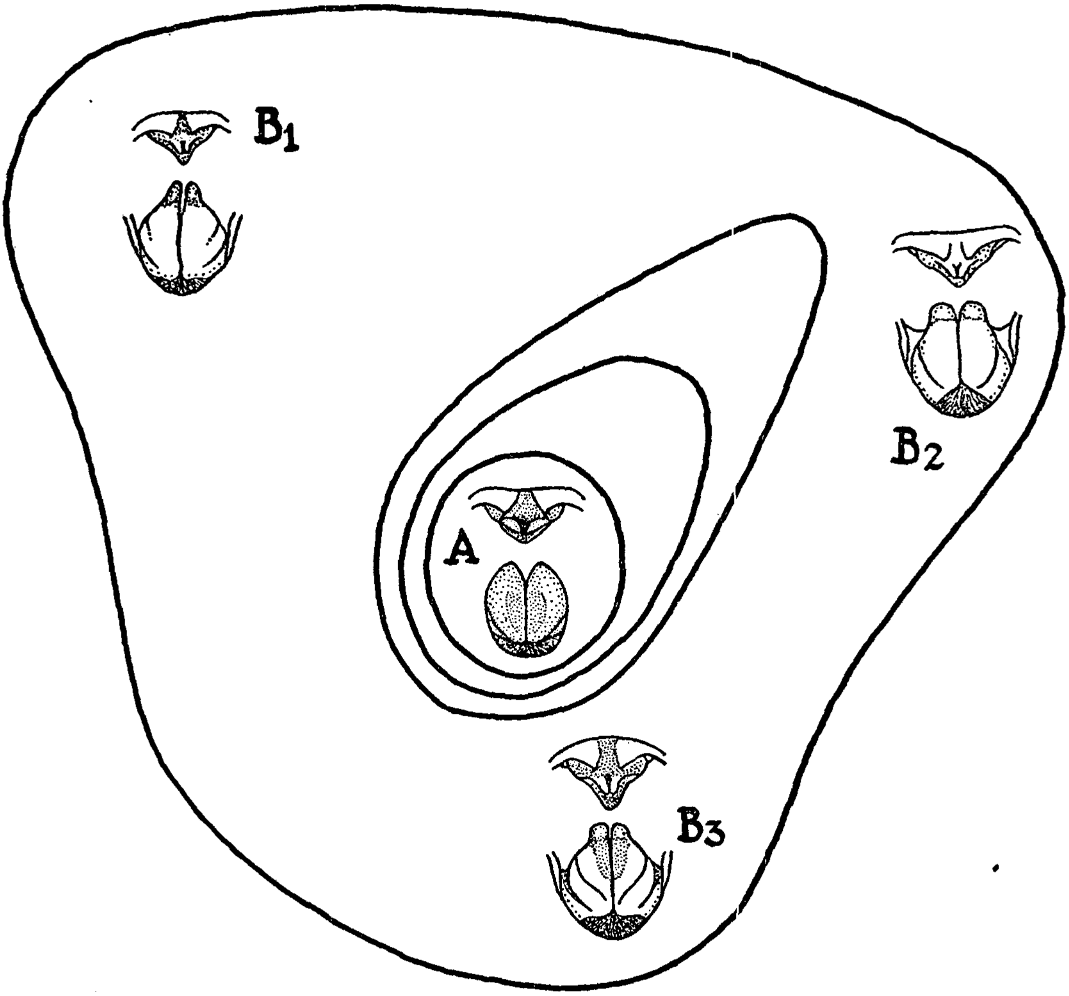

FIG. 8. GEOGRAPHICAL VARIATION OF TWO GENITALIC CHARACTERS IN THE NORTH AMERICAN CAMEL CRICKET, *CEUTHOPHILUS UHLERI*

Population A, in north-central Alabama, has the apices of the epiproct (upper figure) and subgenital plate (lower figure) unconstricted and the marginal thickenings of the former separate and divaricate. In peripheral population B the apices of these structures are constricted and the marginal thickenings of the epiproct are approximated and subparallel distad. B_1 (Indiana), B_2 (Maryland), and B_3 (west Florida) differ in size and robustness, but are much more like each other than any of them is like population A. Isophenes may be drawn between the center and periphery of the range approximately as shown, the axis of elongation being along the Appalachian Mountains. (After Hubbell, 1954.)

habiting Indiana, Maryland, and Florida are more similar in respect to these features than any of them is to the central population in northern Alabama. The isovariant lines or isophenes form contours centering on northern Alabama and running out along the Appalachian axis. Superimposed on this cline of covariant characters is another, a north to south increase in size, which tends to obscure the resemblances of the peripheral populations. . . . An attempt to apply conventional nomenclature to this situation would have resulted in a peripheral subspecies extending from Florida to Iowa to New York in a ring around a central subspecies, which seems absurd.

African Squirrels

If only as a warning against too facile an interpretation of central-peripheral variation, we should perhaps include an example that can be handily explained on purely ecological grounds, just as well as along the lines we have been exploring.

The squirrels of the genus *Heliosciurus* have been referred to as many as 45 subspecies distributed among a maximum of 11 species. Ingoldby (1927) considers that all of these populations constitute a single species inhabiting Equatorial Africa, but one varying strongly in size and especially in color over this wide area. The variation assumes a somewhat concentric pattern centered in the Congo rainforest, and remote samples from around the savannah periphery often resemble each other much more closely than they do the central forest strains. There is complete intergradation from the rainforest areas through lighter woodland and savannah to grassland types. In this case, the central-peripheral pattern may be due entirely or chiefly, as Ingoldby suggests, to close local adaptation following the vegetation types, which also run somewhat concentrically around the Congo. This squirrel is a promising subject for further and more detailed study.

In the examples cited above, the emphasis has rested on variation known or thought to be confined to single species. In each case, some theoretical expectation of central-peripheral differentiation appears to have been fulfilled. In a few cases, perhaps, the differentiation can be correlated more or less closely with concentric vegetational or other ecological zones (*Heliosciurus*), but certainly the other examples cannot all be easily linked to environmental gradients. Central-peripheral variation has been repeatedly discussed before, the apparent lack of environmental correlation duly noted, and the cause even laid to "*Alleldiminution*" through "*Elimination*" (Reinig, 1939), or to "the instability of certain genes and the loss of alleles in the border populations of an expanding species" (Mayr, 1942, p. 96). Such interpretations seem to come under the general "distance effect" or "geocline" concept sometimes discussed in taxonomic papers. Mayr, however, believes that in these cases "selective factors are involved to some extent."

Various ideas and data more or less closely related to the present hypothesis are apparently widespread in the literature (e.g. Matthew, 1915; Lutz, 1916, Timoféeff-Ressovsky, 1940, among others), and it would be interesting but difficult to trace the historical continuity of thoughts along this line. For instance, there is the venerable notion that variation in the genus *Homo* has proceeded prevailingly outward from more central continental areas into peripheral Europe, riding on successive population waves. There seem to be no serious objections to this point of view. It may well be that speciation in early man depended on central-peripheral processes as outlined in the present hypothesis. In fact, I predict that good evidence for this will be available in a very short time.

With the phases of contraction, populations of the species disappear from the peripheral areas, except in relatively restricted refugial pockets or islands that are favorable enough to allow survival of some expansion-phase remnants. At this stage, or course, the central populations are geographically isolated from the peripheral remnants, so as to permit the expected accumulation of genetic differences between them.

I do not think this point requires much documentation. Every taxonomist and field ecologist should be able to call up his own examples of range contraction, and of animal populations isolated from their main species range. We have already reviewed several relevant cases. Such populations may or may not show detectable differences from one another, but there can be little doubt that they do differ genetically in some ways, even if only in the frequencies of one or a few alleles.

When differences appear in peripherally isolated populations, they are often more or less obviously adaptive to the local environmental conditions. They can also represent visible side (pleiotropic) effects of cryptic adaptive characters, such as physiological or behavioral ones. Perhaps we must also consider random fixation and gene loss, but as studies of field populations accumulate, these processes seem ever less significant as forces in evolution.

Unfortunately, under the "subspecies method" of describing geographical variation, the local characters peculiar to isolated populations are usually emphasized, and broad interpopulation similarities are often neglected. In this way, major trends and patterns of variation are nearly always masked to some extent in taxonomic papers. And on one occasion, I was told by a competent herpetologist that he had spent much time analyzing the geographic variation of a common snake species, only to end by shelving the project and the data for the reason that "the races were not clear-cut enough to name!" For a fuller critique of the subspecies concept, see Wilson and Brown (1953).

In spite of the serious difficulty one encounters in attempting to extract relevant information from a subspecies-oriented literature, we have seen in the last section that central-peripheral patterns of variation (centrifugal geoclines?) do occur widely, often cutting across the more obviously and simply adaptive clines (ecoclines) or local character-types (microraces). This central-peripheral differentiation exists in theory even for completely continuous populations (see Fig. 1), but it can be the basis for species separation only if geographical isolation intervenes to block gene flow (Mayr, 1942).

During the contracted phase, of course, even the central populations may become fragmented or patchy in distribution, as has been stressed repeatedly by Sewall Wright and other authors. This is especially true in very favorable areas, such as tropical rain forest, where "mosaic" distributions tend to be determined more by biotic than by physical environmental factors. Under such conditions, gene complexes presumably can develop "coadaptedness" and can come to prevail in particular demes, both central and peripheral. Interdeme competition and selection (Wright, 1956) can be expected to become increasingly effective after the populations enter the phase of density increase and expansion.

If, as must happen in only a small proportion of cases, the differences mount to the point of reproductive isolation, the next phase of expansion will establish the geographical contact needed to confirm the new species difference. The new, contiguous or overlapping species will likely be forced to avoid hybridization (through reinforcement of the reproductive barriers) and competition (through ecological or geographical displacement). The chances are that, in most such contacts, the "new central" species overwhelms the "old peripheral" species by competitive pressure, or, more likely, by means of adaptations of the general "aggressive" type, functioning to remove or incapacitate competitiors. But if the two new species can specialize to divide the exploitable environment between them, they may both persist.

It seems likely that most expansions find reproductive isolation between central and peripheral elements not complete enough to prevent swamping when geographical contact is reestablished. The alternative possibility is that species arise very frequently, but that the peripheral ones are wiped out by competition or aggression at an almost equal rate. Probably not more than a fraction of the range fluctuations suffered by a species can produce successful, indefinitely self-maintaining daughter species. Otherwise, the number of animal species would be vastly greater than it is. We do know that centrifugal swamping exists, as in the case of the imported fire ant, but it does not seem possible at present to guess at the proportion of cryptic "trial species" that may survive for a few generations and then succumb, unnoticed by even the most eagle-eyed taxonomist or population geneticist. For an interesting "trial species" situation in the plant genus *Clarkia*, see H. Lewis (1953).

But in at least a small proportion of contacts, there will exist differences of the sort that add up to reproductive isolation between relatively successful populations. In such cases, reinforcement of the isolating mechanisms will normally develop. To the extent that all or some of the same differences tend to be preadaptive for different niches, the two populations will diverge further along these same lines in order to minimize competition between them. These two processes add up to character displacement, a subject reviewed in detail by Brown and Wilson (1956).

Character displacement means that differences between closely related species will normally tend to be greater where they occur together (sympatrically) than in populations of either occurring apart from the other. We should expect to find character displacement arranged on a central-peripheral basis, and indeed such examples appear to exist in the crossbill and the *Drosophila pseudoobscura* subgroup, discussed below.

Ecological displacement may of course tend to lead to differences in spatial distribution, or geographical displacement. In some cases also, geographical displacement will occur when two newly reproductively isolated species have so nearly identical ecological requirements that their ranges can meet without either species being able to penetrate significantly into the area of the other (summary of cases in birds by Vaurie, 1955).

In accordance with the concept of geographical displacement and the expected higher evolutionary potency of centrally evolved species, we should expect to find the central-peripheral pattern extending to pairs of closely related species. This pattern will be obvious at first only in those cases where range expansion is free to develop in all, or at least in several, compass directions. We must look for such cases in the reported "fringing" and widely discontinuous species ranges, of which a few are examined below.

The Crossbills

Were I an ornithologist, I think that the finches of the genus *Loxia* would take up most of my research time. No group of birds seems to offer more tantalizing problems in that area of biology where systematics, ecology, zoogeography, population dynamics, and ethology overlap.

The density-reactive irruptions of the crossbills have already been discussed. It may now be useful to mention some features of the taxonomy and distribution of these birds. Of the three main types, *L. pytyopsittacus* has a very deep, parrot-like bill (Fig. 9A) and is restricted as a breeder to countries around the eastern Baltic Sea. Apparently its thick bill is correlated with its preference for the seeds of pines as a diet.

The white-winged or two-barred crossbill, *L. leucoptera,* breeds from northern Scandinavia eastward through boreal Eurasia and the northernmost American forests. In Europe, at least, it is said to prefer the seeds of larch, and its bill is generally weaker than in the other kinds of crossbills of the same or nearby areas. In the mountains of Haiti and the Dominican Republic there are isolated populations of crossbills (*L. megaplaga*) very similar to *L. leucoptera,* to which they are customarily attached as a race. These probably feed chiefly on pines, the mountain conifers of Hispaniola, and the bill is correspondingly thicker than in the nearctic *L. leucoptera.*

The dozen or more named populations usually considered collectively as *L. curvirostra,* the "red crossbills," breed very widely in the coniferous forests of Holarctica, especially in those regions not or thinly populated by *L. leucoptera.* Many populations of *L. curvirostra* have medium bills (Fig. 9C) and tend to feed mainly on spruce, fir, and pine, their preference varying in different populations. Others have deep bills (Fig. 9B) intermediate between those of "typical" *L. curvirostra* and *L. pytyopsittacus*: *L. anglica* (=*scotica*) breeds in Scotland, *L. balearica* in the Balearic Islands, *L. poliogyna* in North Africa, *L. guillemardi* in Cyprus, *L. estiae* on Oesel Island in the Baltic, off Estonia, and there is a similar type in the Crimea. The chief food of these intermediate-thick-billed forms is known or presumed to be pine seeds. It should be noted that these intermediate bill types are situated peripherally to the main European crossbill populations. Griscom considered that the intermediates signified conspecificity for *L. curvirostra* and the thick-billed forms, including *L. pytyopsittacus*, but all of these intermediates can now be considered either as distinct species or as undisplaced peripheral populations of either *L. curvirostra* or *L. pytyopsittacus* when viewed in the light of the character displacement theory (Brown and Wilson, 1956). Especially is this so when we recall that L. *curvirostra* and *L. pytyopsittacus* breed, apparently without intergrading, in the same general areas.

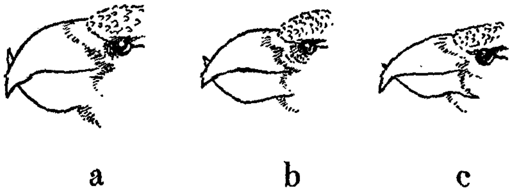

FIG. 9. CHARACTER DISPLACEMENT IN BILL FORM IN EURASIAN CROSSBILLS, GENUS LOXIA

A, *L. pytyopsittacus* from Uppsala, Sweden. B, *L. pytyopsittacus* or *curvirostra*: intermediate form from Scotland. C, *L. curvirostra,* "typical" form, from Bashkiria, Ural Mts. (Adapted from Kirikov, 1940.)

The pattern of geographical variation in the crossbills, at least in the absence of more detailed analysis of particular characters, seems to be roughly one of zones of differing bill depth alternating from the center in northern Europe outward. The North American red and white-winged crossbills both average smaller in body size and have smaller bills than their European counterparts, but size and bill depth recover to nearly or quite the status of European *L. curvirostra* in the Mexican populations of this same species. A similar situation exists in southeastern Asia, terminating in the Annamite population. Such alternation has already been mentioned above in the variation of the drongo *Dicrurus leucophaeus.* It may even often be true that waves of characters proceeding outward from the center tend to contrast, each with its predecessor, perhaps as a result of varying degrees of character displacement. These cases need close study before we can say much more about the nature, let alone the causes, of central-peripheral *character alternation.*

Divergent extralimital red crossbills inhabit the Himalayan region, southern Annam, northern Luzon, and Newfoundland; the last two populations (*luzoniensis* and *pusilla*) may well be distinct species. With the British and isolated Mediterranean resident strains, these peripheral populations indicate that emigrants can and occasionally do permanently establish themselves far beyond the normal breeding range. We know that crossbill populations frequently disappear from peripheral areas where they have bred and increased for a number of successive years. Apparently this is true of the crossbills that flourished and spread in Ireland after the irruption of 1887, and it may apply also to populations in the southern Appalachians, parts of Spain, and elsewhere.

We need much more information on the crossbills. Especially required are observations on the pairing specificity and behavior in areas and at times when two or more morphological types are breeding together; these could possiby be supplemented by laboratory breeding experiments. Also needed is a more complete and detailed comparative account of feeding habits for all the recognizable populations, linked with a new quantitative study of bill size and shape as independent variates for all the crossbills.

But even with the incomplete evidence we have at the moment, the crossbills seem to provide nearly all the features one might expect of a widespread and actively evolving species group or species-succession of the centrifugal type (data chiefly from Griscom, 1937; Kirikov, 1940; Lack, 1944).

Sibling Species in Drosophila

In western and southwestern North America occurs the much-studied *pseudoobscura* subgroup of the *Drosophila obscura* group. This subgoup includes four extremely close species: *D. pseudoobscura*, *D. persimilis*, *D. miranda*, and *D. frolovae*. *D. frolovae* is recorded only from the type locality in Michoacan, Mexico, and practically nothing is known about it. *D. miranda* is a rare species restricted to the Pacific Coast area (see map, Fig. 10). *D. persimilis* is more common and has a wider range, but is also a Pacific region endemic. *D. pseudoobscura* is widespread in Mexico and western North America, blanketing the ranges of *D. miranda* and *D. persimilis*, except that *D. persimilis* extends a little farther north and west in British Columbia and reaches higher elevations in the mountains where both species occur in the same general region.

D. pseudoobscura and *D. persimilis* overlap broadly in local distribution and ecological preference, and the two species commonly breed side by side in the same sap fluxes, so that some competition is apparently inevitable. Their relative abundance fluctuates seasonally and over the years, but *D. pseudoobscura* seems generally to predominate.

D. miranda has a third chromosome arrangement very like the Hypothetical primitive type, whereas in *D. pseudoobscura* and *D. persimilis*, the homologous third chromosome is highly polymorphic in arrangement (Dobzhansky and Epling, 1944, summary in Patterson and Stone, 1952, pp. 18–20, 53–54, 191–199, figs. 35, 55–58).

Although from morphological evidence it seems that the *pseudoobscura* subgroup is most closely related to some Palearctic members of the *obscura* group, one might judge that the subgroup has been in the New World for a long time. Certainly it has undergone and is now undergoing active evolution in western North America. In my opinion, its present main center of evolution probably lies in the southwestern United States and northern Mexico. *D. pseudoobscura* occupies this center and areas peripheral to it. The Pacific Coast States constitute a strip of favorable territory, but one that is smaller and probably to be considered peripheral, on the whole.

The country lying between the Sierra Nevada of California and the Rockies is for the most part relatively unfavorable for occupancy by the *D. pseudoobscura* subgroup, and *D. pseudoobscura* populations living here lack some inversions found on either side. It seems likely that this general region marks more or less precisely the previous gap that must have separated the incipient *D. pseudoobscura* stock from the *D. persimilis* stock for long enough to allow reproductive isolation to develop between the two. It is *D. pseudoobscura* that has subsequently been able to cross the gap, doubtless on the crest of more than one "population-wave."

To me, the *pseudoobscura* subgroup looks like a fairly typical central-peripheral situation involving at least three "species-waves" as represented in the order *miranda, persimilis, pseudoobscura.* In addition to the general distributional pattern of the three species (and perhaps also *D. frolovae*), we have other scraps of possible evidence mentioned in passing by Dobzhansky and Epling (1944).

First, it has been found that sexual isolation is stronger between *D. miranda* and *D. persimilis* than between *D. miranda* and *D. pseudoobscura*, suggesting that the former pair have been sympatric for a longer time. Second, the abundance of *D. pseudoobscura* increases in general as one goes from the Pacific Northwest toward the east and south. This

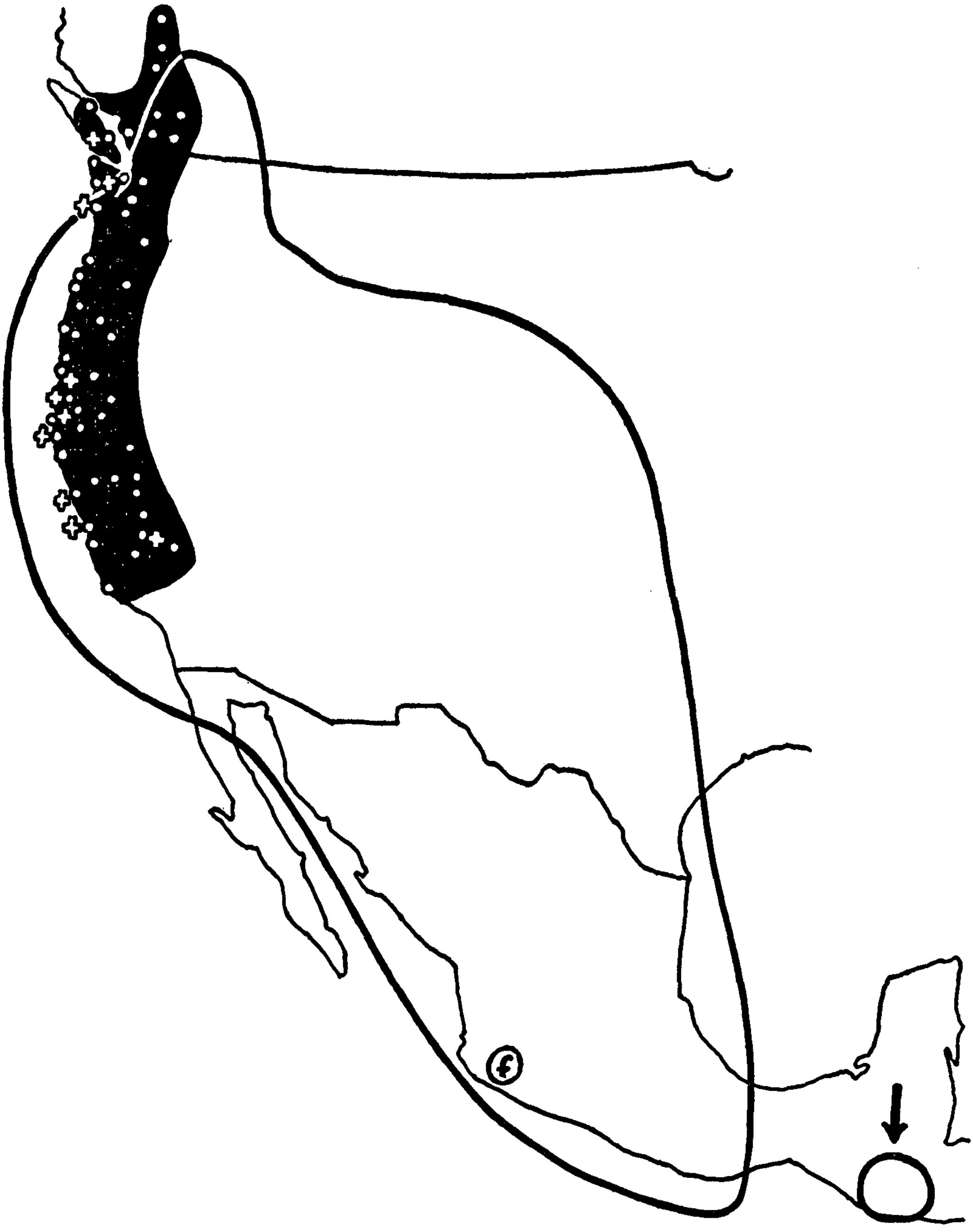

FIG. 10. MAP SHOWING THE RANGES OF THE FOUR SPECIES OF DROSOPHILA OF THE *D. PSEUDOOBSCURA* SUBGROUP IN WESTERN NORTH AMERICA AND GUATEMALA

The approximate limits of the range of *D. pseudoobscura* are indicated by the heavy lines. The approximate range of *D. persimilis* is indicated by solid black (individual locality records as of 1944 are round white dots). Locality records for *D. miranda* are marked by small crosses, and the sole locality for *D. frolovae* by an encircled letter "f." (From Dobzhansky and Epling, 1944, and other sources.)

may be correlated in part with temperature and moisture gradients, as suggested by Dobzhansky and Epling. Third, there exists a certain type of Y chromosome ("type I") that occurs

> . . . in most populations of *persimilis* and also in certain populations of *D. pseudoobscura*. Judged superficially, this fact might be taken as evidence of introgression. This chromosome type, however, has never been found in the populations of *D. pseudoobscura* from California, Oregon and Washington, where it would be expected because of the presence of *D. persimilis*, but only in populations found in southern Arizona, Mexico, and Guatemala, far removed from the range of that species. The type of Y chromosome is similar in appearance in the two species, but it is not impossible that in reality the chromosomes in question are different. If they are in fact genetically identical, any hybridization must have taken place in the remote past.

This Y chromosome situation seems to qualify as a further case of character displacement, comparable to the example already given of the bill depth in crossbills. It would be interesting to know what, if any, adaptive correlations this chromosome character has.

Dobzhansky (1956) has reviewed and added to the data available concerning fluctuations in the frequency of third chromosome inversions in *D. pseudoobscura* and *D. persimilis* in California. These gene arrangements show fairly regular seasonal shifts in relative frequency of occurrence, so that a given one may predominate during a given month in most years. There are also longer-term rises, falls, and repetitive fluctuations in frequency of individual arrangements. It now begins to appear that at least some of the frequency shifts in third chromosome polymorphs are reactive to density changes in the fly populations, especially in view of the recent findings of Birch (as cited by Dobzhansky) relative to the Standard and Chiricahua inversions.

Since 1945, an inversion known as Pike's Peak (PP) has become increasingly common in *D. pseudoobscura* populations of California. Before that date, PP was known only as a rarity in central California, and was not found in California localities where it later became frequent. Previously, PP had been more common in the Rockies, in Texas, and in northern Mexico. Dobzhansky thinks it unlikely that the California rise is due to the "introduction of PP chromosomes into California from elsewhere," but the basis for this belief is not clear to me.

There seems to be no outstanding reason why PP or any other inversion should not be expected to increase its area of occurrence, granting that it is adaptively positive. Surely, it must have spread at some time, even if not initially during the years immediately before and after 1945. It is also possible, of course, that PP has arisen to prominence in California because some of the genetic material it presumably holds together has changed in an adaptively positive way. Such a change would still have a geographic origin and would tend to increase its geographical range.

To my way of thinking, at any rate, there exists the possibility that either PP or some potent constituent now associated with this inversion is currently spreading from (perhaps) a Texan or Mexican area of origin. Considering the opportunities open for long-distance transport of *Drosophila* propagules (Dobzhansky and Epling, 1944), the observed (probable) rate of spread is unremarkable. It would be interesting to study dispersal, emigration, and colonization of *D. pseudoobscura* under differing population densities in nature.

There is some direct evidence to indicate that dispersal is density-reactive in this species and in *D. persimilis*. Carson (1951) found in California that adults of these species, when visiting their favored natural feeding and oviposition sites at slime fluxes on the trunks of *Quercus kelloggii*, tended to avoid fluxes already containing older larvae or pupae of *Drosophila*.

Fringing Forms in European Bumblebees

"*Fringing distribution*" is a term proposed by O. W. Richards (1935) and applied to the populations themselves as *Randformen* by Zimmermann (1950). Richards studied the European distribution of two very closely related species of bumblebees of the *Bombus agrorum* group. *B. muscorum* ranges in Europe from Rumania, Turkey, Italy, and Spain northward to the Baltic, and through England, Scotland, and Ireland. *B. smithianus* occurs on certain of the islands fringing the coasts of England, Scotland, and Ireland, in particular those where *B. muscorum* is absent. The two species have been taken at Ross in western Scotland, but they seem here to be elevationally separated. The Hebrides, Shetlands, Faroes, Norway, and Finland have *B. smithianus*, which continues around through the Archangel district and southward into Russia for an undetermined distance. Richards compares this distribution with that of some microtine rodents of Europe (discussed below) and favors the explanation that *B. smithianus* is being overtaken by the more centrally-placed *B. muscorum*, which is able to replace *B. smithianus* when it meets it. Richards suggests that the chief point of competition could be for nesting sites, usually old nests of voles. He also indicates that *B. muscorum* itself may be under increasing pressure from other common and centrally-placed members of the same (*agrorum*) species group, since *B. muscorum* tends to be abundant only when occurring apart from these.

New World Butterflies of Genus Euptoieta

The fritillaries of the genus *Euptoieta* range from temperate North America to southern South America. There are two close but distinct superspecies, *E. claudia* and *E. hegesia*.

E. claudia is resident in the United States and in Mexico, Guatemala, and Jamaica at higher elevations. A very similar form, *hortensia*, is usually placed as a race of *E. claudia*; this form is found in Bolivia, the La Plata Basin, and neighboring mild regions. Other *claudia*-like populations occur in upland Ecuador, Colombia, Panama, and Costa Rica, and these are generally held to represent another very close species, *E. bogotana*, in superspecies *claudia*.

E. hegesia ranges from the southern extremities of the United States southward through the West Indies, Mexico, and tropical South America, mostly at lower elevations. Where it meets the range of *E. claudia*, as in Mexico, Jamaica, Guatemala, and at the northern and southern borders of its range, *E. hegesia* shows only slight distributional or altitudinal overlap with *E. claudia*.

The two superspecies feed as larvae on the same general food plants, mainly of the Passifloraceae and Violaceae. There is little doubt of their close relationship, and it would be interesting to know whether the ranges of either or both species are expanding or contracting.

Neotropical Dacetine Ants

The distribution of the small but common ant *Strumigenys louisianae* closely resembles that of the *Euptoieta claudia* superspecies, except that it is more widespread in the Greater Antilles. *S. louisianae* is replaced by a very similar species, *S. unidentata* Mayr, in Amazonas and central Brazil, and the two overlap, so far as known, in southeastern Brazil.

Melanesian Ants of Genus Anochetus

E. O. Wilson has called to my attention the distribution of ants of the *Anochetus cato* group in New Guinea and surrounding archipelagoes. Diagnostic characters, variation, and synonymy of the *cato* group are outlined in a manuscript to be published eventually by Wilson. New Guinea proper, the Bismarck Archipelago, and the Solomon Islands as far as San Cristobal are inhabited by *A. cato* Forel, apparently a single species that varies strikingly in color from one part of its range to the next (i.e., is "polytypic"). Closely related to *cato*, but differing by a clearcut sculptural character, are four populations comprising "superspecies *isolatus*." These are: *isolatus* Mann (Santa Cruz Islands, and relatively rare on Malapaina Island in the Three Sisters Group, near San Cristobal, where it coexists with *cato*); *splendidulus* Yasumatsu (Truk); *seminiger* Donisthorpe (Waigeo Island, off the Vogelkop), and *splendens* Karawajew (Aru). Aside from color and perhaps one or two other slight differences, these four peripheral forms are very close, and it is entirely possible, in view of the uncertainty principle, that some or all of them are still conspecific, instead of being superspecies members. Wilson has retained the four as species only by arbitrary designation.

While undoubtedly there remain unsampled many populations of both *A. cato* and the *A. isolatus* superspecies, the pattern as seen from the present material is certainly suggestive of a central origin and centrifugal spread of *A. cato* at the expense of the *isolatus* type.

Another similar case among Melanesian ants involves *Strumigenys szalayi* Emery (New Guinea) and the very similar *S. australis* Forel (northern Queensland, Micronesia, Philippines).

Palearctic Wagtails

The birds of the yellow wagtail complex have been studied by Williamson (1955), who recognizes two species, *Motacilla lutea*, representing the greenish- or yellow-headed populations, and *M. flava*, for the populations in which the head is more or less blackish, gray or bluish. (But see Mayr, 1956).

M. lutea breeds in three separate areas: (1) Britain and isolated pockets on the Atlantic coasts of France, Holland, Heligoland, and Norway; (2) the Kirghiz Steppes, from the Volga River, and the Caspian and Aral Seas eastward to the headwaters of the Yenesei River; (3) Lena River eastward to Sakhalin and the Kurile Islands. These areas are on or close to certain boundaries of the distribution of *M. flava*, which has a much more extensive range in northern Eurasia (extending even to Alaska in the east) and is widespread in the Mediterranean area. Williamson agrees with Johansen, an earlier reviser, in

> . . . regarding the yellow-headed populations as the most primitive, and the dark- and blue-headed forms as derivatives of interglacial and postglacial origin whose subsequent spread has confined the yellow-headed birds to somewhat restricted ranges.

Microtine Rodents of Europe

Zimmermann (1950) discusses the *Randformen* of the rodents *Clethrionomys glareolus*, *Microtis agrestis*, *M. arvalis*, *M. oeconomus*, and *Arvicola amphibius* in Europe. In each of these cases, the central European population tends to be smaller in size. The peripheral populations on small offshore islands or in Britain, the Iberian Peninsula, and Scandinavia are larger and tend to be alike in size despite the considerable climatic differences occurring over the fringes of Europe where they occur.

The bank vole, *Clethrionomys* (=*Evotomys*) *glareolus*, has interested several authors (Hinton, 1926; Zimmermann, 1950; Steven, 1953) because of its peculiar distribution and variation. This superspecies is distributed over much of temperate and boreal Holarctica (as *rutilis*, *gapperi*, etc., in North America). In Europe there exist, roughly speaking, two extreme forms. *Glareolus* is smaller, usually has the reduced *simple* type of upper third molar, and is frequently lighter in color; it is the common lowland form over most of the continent and (as the scarcely differentiated "race *brittanicus*") on the mainland of England and Scotland. Larger forms, which for convenience can be grouped under the name *nageri*, have predominantly the *complex* type of upper third molar, are often rather dark in color, and are distributed chiefly in peripheral islands and, on the continent, in high mountains. Various degrees of morphological intergrades are known from place to place.

Large size seems to be the most consistently peripheral of these characters; tooth type is less regularly so, and dark coat color is only rather erratically associated with the periphery of the range.

It is puzzling that Hinton considered *glareolus* closest to the primitive type of the superspecies, when his evidence indicates, at least to me, that *nageri* or something like it may have been the earlier form. And when Hinton comes to speculate on the past movements of the forms, he has *nageri*-like waves moving outward first, to be overrun by later arrivals of the *glareolus* strain. He describes from Britain *nageri*-like Pleistocene fossils, and Post-Glacial remains that are most like the present *glareolus*, whereas present British mainland voles are all *glareolus* ("*britannicus*").

Zimmermann felt that the peripheral *nageri*-like populations were the survivors of an old, wide-ranging type in process of being replaced by a related strain from the center outward. He considered, however, that all of the forms concerned belonged to a single species.

Steven (1953) studied the British representatives of this complex. These include a widespread population of a smaller, lighter type ("*britannicus*") with predominantly simple upper third molars (very close to the "nominate race" of *glareolus* from the continent) inhabiting the British mainland and only a few close-in islands.

Three other disjunct minor populations occur on islands along the western fringe of Britain: Raasay and Mull in the Inner Hebrides, and Skomer farther south. These three populations all consist of voles significantly larger than the mainland ones; two of them (Mull and Raasay) are darker in color; and two of them (Skomer and Raasay) have a majority of upper third molars of the complex type. The color and molar characters appear to be unifactorial.

Steven made some crosses between these populations. The crosses Mull male × Skomer female and Skomer male × Raasay female "have so far been carried through more than a single generation, and show no sign of hybrid sterility, rather the reverse." This is interesting in view of the great distance along the British west coast separating Skomer from the Inner Hebrides.

Three other crosses, Skomer male × Mull female, Raasay male × Mull female, and Mull male × *britannicus* female, produced offspring, but further results awaited the maturity of these young at the time of his writing. Steven was unable to rear young from the Raasay male × *britannicus* female, an interesting result in view of the fact that these two parent strains are the only ones that differ by all three characters: size, color, and third molar type. Steven thinks that

> . . . the variety of hybrids already obtained, namely, half the total number of combinations possible, makes it unlikely that speciation has proceeded as far as a sterility barrier in any case, though there may be a partial one between the island and mainland stocks, since these crosses have been much more difficult to make than inter-island ones. We are not yet in a position to say why this should be so or to express it quantitatively. It may simply be a case of difficulty in mating associated with the size difference, but it may equally well be based upon a marked difference in temperament. It has been very noticeable that while all the island stocks become relatively docile, *britannicus* remains extremely wild and shy and difficult to handle even after many months in captivity.

The emphasis here upon the "sterility barrier" is explicable when Steven later says, "I do not now think we can reasonably regard [the Hebridean populations] as more than well-differentiated subspecies." Evidently his criterion for the species gap is more strict than is customary, for, if his limited observations are borne out, a rather distinct reproductive barrier may well separate the peripheral populations from the mainland ones, but possibly not from each other.

Steven apparently rejects the "relict" theories advocated by Hinton and by Zimmermann to explain the peripheral and alpine distribution of the "*nageri* group" forms, but his reason for doing so is never explicitly stated, at least so far as I can tell. He prefers to believe in a polytopic origin of the three peripheral British strains "during the past few thousand years from a common stock with *C. glareolus britannicus*," but he does not support this belief with significant evidence. It seems to me that Steven's data, admittedly still preliminary in 1953, do more to support the relict theory than to oppose it.

My friend Dale Osborn tells me that cases of central-peripheral distribution of characters may not be rare in small North American mammals. He instances the northern shrews of the *Sorex arcticus-tundrensis* complex, which may represent a single species. The shrews from Nova Scotia and Alaska tend to have light brown backs and light buffy sides, while those from southern Labrador and central Canada are dark- or blackish-brown on the back and light brown on the sides.

Bipolar Distributions of Marine Animals

Certain distributional phenomena found among marine animals may indicate that central-peripheral speciation is active in the sea. Numerous interesting cases are mentioned by Ekman (1953, pp. 249–263) in his very full discussion of *bipolarity*, a term that covers the distributions of species (or genera and families) with ranges in higher latitudes of both Northern and Southern Hemispheres, but which do not occur in intervening warmer zones. Sometimes the same or "twin" species or genera have a bipolar distribution, and related species or genera fill in through the tropical seas between, a condition Ekman calls "masked bipolarity."

> There is among the Challengeriidae (Radiolaria) a deep-water form, *Protocystis sloggetti*, which is mainly domiciled in the equatorial oceanic regions of the Atlantic and Indian Ocean between 40° N. and 40° S. and may be caught most frequently between 400 and 1500 m. In cold seas, in the north as well as in the south, it is replaced by the distinctly bipolar *P. harstoni*, which is common in these seas and which prefers the upper layers of water, although it has also been found alive at a depth of 4000 to 5000 m. *P. harstoni* has probably developed in both the cold-water regions by adaptation to similar environmental conditions from an equatorial ancestral form, closely related to or perhaps identical with *P. sloggetti*. . . .
>
> A similar explanation may, according to Michaelsen, be given for the position of two independent although very closely related species of ascidians, namely *Botrylloides leachi* and *B. nigrum*. The former occurs in the North Atlantic (Norway to Mediterranean) as well as in the southern hemisphere off South Africa, West Australia, New Zealand and the Aucklands, while *B. nigrum* lives in the tropical part of the East and West Atlantic, the Indian Ocean and the West Pacific.

In still other cases, such as that of the foraminiferan *Globigerina pachyderma* and its tropical form *dutertrei*, similar bipolar types are clinally linked to intermediate tropical populations and are thus demonstrably conspecific. Ekman feels that these examples arise through "*bipolar taxonomic parallel development*."

What percentage of such cases is genotypically, not phenotypically, determined is at present uncertain. Among the genetically based cases independent (polytopic) origin and parallel evolution of some bipolar characters under the pressure of similar cold-water environments is of course one possibility. Another possibility is that the bipolar populations represent the peripheral relicts of an old, widespread population that has undergone a central change or suffered central replacement (Théel, 1886; Strohl, 1936).

CONCLUDING DISCUSSION

The most significant parts of the hypothesis are the emphasis on the center as the principal source of evolutionary change leading to "potent" new species and higher categories, and the role of population density fluctuations in spreading characters and making and breaking the contacts between populations.

As has already been emphasized, there is nothing new in the idea of evolution by central change, and centrifugal spread of change. I have already suggested that even if we assume a species range within which there exists complete uniformity of environment, population density, and distribution, and rate of spread of different adaptive genetic changes—even then we can expect a differential to develop between the geometric central and peripheral areas of the range (see Fig. 1).

When we substitute a natural species distribution for such an ideal model, the irregularities introduced are of overriding importance so far as the origin and spread of genetic change are concerned. However, it seems that these irregularities even more strongly favor differentiation of central from peripheral populations, provided that we now think of "central" areas primarily in terms of their overall carrying capacity and reliability as permanent breeding grounds, rather than in the narrow geographical sense. Of course, where there is no serious asymmetry in the positions of the physical and biotic barriers determining the distribution of the species, we expect to find reasonable correspondence between the two kinds of centers—geographical and evolutionary. This correspondence is apparent in several of the examples discussed. In cases where distributional limits are asymmetrically placed, such as those in which the most favorable part of the breeding range of a terrestrial animal is close to one coast of a continent, or crowded by high mountains, the evolutionary center may seldom be near the geographical center of the range. In this sense, species ranges are probably more often asymmetrical than not.

Despite asymmetry, the active evolutionary center of a species range may often be located more or less exactly by observing relative population densities at different points, by determining the source or direction of any emigrations, and by plotting the geographical variation of the species and the ranges of related species. One expects this center to be both broad and indefinite, and to have had a history of shift and change.

The currently favored models of geographic isolation leading to species separation are those involving simple division of the range and colonization across barriers. While no doubt simple division and colonization processes can and do lead to specific separation, it is difficult to regard species that may have been formed in one of these ways as the main source of further evolution.

Probably the division type of speciation is exemplified most often by the east-west species pairs in Eurasia and North America, thought to be the resurgent survivors out of Pleistocene refugia. The trouble with such cases is that many of them can be interpreted in alternative ways (Mayr, 1942, pp. 177–180). There often is no good reason why such species pairs may not represent two waves of populations coming from the same direction.

Colonization speciation has been discussed by Mayr (1942), especially under the heading "Double Invasions" (p. 173). The concept of double invasion has much in common with the present hypothesis, except that Mayr seems to stress differentiation of the insular isolates rather than of the continental source populations.

Mayr later (1954) developed the colonization idea into his hypothesis of "typostrophic" speciation, which emphasizes the probability of marked changes in the selective value of genes against the altered "genetic environment" of peripheral colony-founders as compared to that of the source populations. In this way, the aberrant nature of some peripheral populations is accounted for, and Mayr suggests that these populations may represent one kind of situation from which new major groups of animals arise. [It is unfortunate that Schindewolf's term "typostrophic" has been brought into speciation discussions and somewhat fixed there (e.g., Hubbell, 1956). Mayr, of course, was using the term in a way very different from the way in which Schindewolf employed it.]

"Typostrophic" changes may occur and may be important in colonial speciation, but it is necessary before accepting Mayr's idea to review the facts and theories bearing on insular colonization and evolution.

It seems likely that Mayr over-minimizes the importance of biotic differences between some of the islands he discusses as populated by colonists. In particular, it is important to ask how the potential competitors and predators of a colonized island compare in numbers and variety with those of the source area and other islands. Lack's work on the Galapagos finches (1947) should demonstrate that this question is of the utmost importance in studying insular variants, and should also prove that it cannot be answered merely by citing general environmental similarities between ranges of different populations.

Further difficulties in Mayr's typostrophe theory have already been mentioned in the introduction. Criticism may be summarized here by saying that this kind of typostrophic change remains to be convincingly demonstrated as an important factor in the evolution of insular species, and that in any case it seems unlikely to have been of much significance as a source of new major groups that are capable of sustained invasion and radiation back into continental areas.

Fortunately, we can learn something about major-group evolution by looking at the distribution of the groups themselves. Following the surveys by P. J. Darlington (1948, 1957), we find that it is likely that most higher-category groups arose in continuous or near-continuous land masses with warm climates, and spread from there to smaller land areas or to those with less favorable climates. The Old World tropics apparently has been the largest of these favorable regions, and the one that has given rise to more dominant, world-spreading groups than any other, at least back through the Tertiary.

Darlington thinks that the large warm areas probably owe their evolutionary potency in large part to their greater chances of producing *general adaptations*—character combinations that confer upon a species the competence to enter a wide variety of environments and prosper in most.

I feel that Darlington's ideas and my own are directly complementary, though we are interested in different levels of the evolutionary hierarchy. If major-group evolution is only the extension and accumulation of normal speciation sequences, as at this moment seems to be the general consensus, then there is no occasion for surprise at the similarity of the central-peripheral patterns produced by the two processes. The only difference expected and found is one of scale.

In order to avoid a misunderstanding of one important point, it may be necessary to reemphasize, first, that the argument presented above is an argument for an hypothesis only, and an hypothesis that requires a great many more facts for its eventual proof or disproof; second, that the kind of speciation here argued is not the only one possible—rather, I think of it as the approximate means by which are produced the species most likely to participate in general phyletic advances.

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